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Neglected *Trichalophus* (Coleoptera: Curculionidae): DNA barcode and phylogeography of high-altitude flightless weevils rediscovered in Southwest China

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Abstract. *Trichalophus* LeConte weevils are rediscovered in Southwest China (Yunnan and Sichuan) after last being collected in 1915. Populations are all found at high altitudes (3704–4158 m) and are attributed to three species: *T. caudiculatus* (Fairmaire, 1886) (= *compressicauda* Fairmaire, 1887, syn. n.), *T. scylla* sp. n. and *T. tibetanus* (Suvorov, 1915). Type specimens of all four species-group names are illustrated. A DNA barcode library of five *Trichalophus* species (29 sequences) is presented at doi: dx.doi.org/10.5883/DS-TRICHAL. All examined species of *Trichalophus* are flightless. Phylogenetic relationships of Southwest China *Trichalophus* based on Maximum Likelihood and Maximum Parsimony analyses suggest their monophyletic origin and monophyly of each species. Results of the temporal analysis are consistent with the basic Quaternary expansion-contraction model of altitudinal range change. The warm period following the Last Glacial Maximum (26,000–19,000 years before present) is linked to the present day high altitude *Trichalophus* refugium in Southwest China, but not for the lineage diversifications, which are much older (8.08–5.17 Mya). An illustrated overview of ten extant Alophini genera is provided.

Key words. New species, new synonym, Yunnan, Sichuan, CO1, Entiminae, Alophini, Father Delavay

INTRODUCTION

The exclusively Holarctic weevil genus *Trichalophus* LeConte, 1876 consists of 51 valid species (Yunakov 2013). Adults of *Trichalophus* are believed to be flightless and brachypterous (Anderson 1997; Fig. 1). Loss of flight ability is commonly observed in a number of unrelated edaphic, alpine, high latitude, subterranean, island, or litter-inhabiting insects. Examples from weevils include Macaronesian *Laparocerus* Schönherr, 1834 (Machado et al. 2008), Polynesian *Rhyncogonus* Sharp, 1885 (Machado 2007), predominantly Oriental *Trigonopterus* Fauvel, 1862 (Riedel 2011), Middle American *Theognete* Champion, 1902 (Anderson 2010), an assemblage of likely unrelated Old World genera historically placed in Molytini (Grebennikov 2014b) and the Western Palaearctic genera of former "Cryptorhynchinae (Lyal 2014) traditionally linked to *Acalles* Schoenherr, 1825 (Astrin & Stüben 2008). The reduced dispersal capacity predisposes such evolutionary lineages to become hostages of their habitats and, therefore, subject to more frequent bottleneck effects. These conditions favour allopatric speciation (Grant & Grant 2006; Ikeda et al. 2012; Vogler & Timmermans 2012) seemingly accompanied by an accelerated rate of DNA evolution (Bromham 2008), as compared to their flight-capable relatives (Mitterboeck et al. 2013). Such biological characteristics make flightless weevils a model group for phylogeographical studies on such dynamic terrains as oceanic islands (Tänzler et al. 2014; Toussaint et al. 2015) or mountaintops (Grebennikov 2014a), if it were not for their often highly inadequate taxonomy. The latter, if not updated, either lacks names for newly detected evolutionary lineages (= new species), or has too many names for the same clade (= synonyms), or a combination of both. In such situations the historical burden of Linnaean names impedes, rather than advances evolutionary studies (Riedel et al. 2013a, b).

The genus *Trichalophus* has a trans-Beringian distribution range, with species found on the Pacific sides of both Asia and North America, evoking the Bering land bridge hypothesis (Berman et al. 2011). All but one species are restricted to either Asia or North America; the exception being the Nearctic *T. hylobinus* (LeConte, 1876) recently reported from North Korea (Yunakov 2013). Trans-Beringian distributions are commonly observed in a number of weevil genera: *Alaocybites* Gilbert, 1956 (Grebennikov 2010), *Thalasselephas* Egorov & Korotyaev, 1977, *Emphyastes* Mannerheim, 1852, *Lepyrus* Germar, 1817, *Lobosoma* Zimmermann, 1964, or *Lepidophorus* Kirby, 1837 (Egorov et al. 1996; Bousquet et al. 2013). Indeed, all but one (Yunakov et al. 2012) Palaearctic records of *Trichalophus* pertain to Siberia, Mongolia, Central Asia and the northern part of the Pacific Asia including Japan, while the Nearctic species are predominantly found in Alaska, the western USA, and Canada west of Ontario (Anderson 2002; Bousquet et al. 2013). Yunakov (2013)

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listed 43 *Trichalophus* species and one non-nominal subspecies (*T. vittatoides striola* Reitter, 1913) for the Palaearctic region, while Anderson (2002) mentioned eight North American congeners. Since then the Nearctic diversity of *Trichalophus* has lost two species names due to synonymy (*T. seriatus* Mannerheim, 1843 and *T. brunneus* Van Dyke, 1927) and has gained two others through the recently synonymized genus *Acmaegenius* LeConte, 1876 (Bright & Bouchard 2008). As a result, eight Nearctic species are currently recognized (*T. arcuatus* Fall, 1907, *T. hylobinus* LeConte, 1876, *T. planirostris* LeConte, 1876, *T. seminudus* Van Dyke, 1938, *T. granicollis* Van Dyke, 1927, *T. didymus* LeConte, 1854, *T. simplex* LeConte, 1876, and *T. alternatus* Say, 1832), the latter four being recorded from Canada (Bright & Bouchard 2008).

Despite the relatively large size of these beetles and their occasional abundance in suitable habitats, biological data on *Trichalophus* are remarkably scarce. Adult beetles appear highly polyphagous (Anderson 2002) being found on a number of shrubs and herbs (personal observation). North American *T. didymus* was mentioned as an occasional pest of strawberries (*Fragaria* sp.) in Washington State (see references in Bright & Bouchard 2008). Immature stages and larval host plants are adequately known only for a widely distributed Siberian species *T. leucon* Gebler, 1841. Larvae of this species feed externally on the roots of *Ribes* L. (Grossulariaceae) as well as on a few other shrubs and take two years to complete development (Krivets & Burlak 1986; Krivets 2006). The host plant record is of potential economic significance, since the host genus includes cultivated currants and a number of ornamental plants. The genus *Ribes* also includes alternate hosts for the White Pine Blister Rust (*Cronartium ribicola* J.C.Fischer, Cronartiaceae), a fungus accidentally introduced to North America about 1900 from Europe or Asia, which causes significant damage to American white pines (*Pinus* spp.; Maloy 2001).

Nothing is known about the evolutionary history of *Trichalophus* and the phylogenetic relationships of this taxon. Flightlessness is not unique for *Trichalophus*, but it is found in some other genera of Alophini (Bright & Bouchard 2008), including the West Palaearctic *Graptus* Schoenherr, 1823 (Davidian & Arzanov 2004). The latter genus has long been known under its synonymous name *Alophus* Schoenherr, 1826 and was widely used in original combinations for Palaearctic *Trichalophus* prior to Reitter's generic revision (1913). No members of either *Trichalophus* or any other Alophini were subjected to a phylogenetic analysis so far. The taxonomic recognition of either the genus or the tribe, along with a few diagnostic characters used in the keys (i.e. Anderson 2002) are, therefore, the only hints of their possible monophyly. Since the genus *Trichalophus* was historically linked to *Graptus*, they both might form a clade, even if paraphyletic with respect to the North American *Plinthodes* LeConte, 1876 (Bright & Bouchard 2008) and perhaps other oligotypic Holarctic genera of Alophini (*sensu* Alonso-Zarazaga & Lyal 1999, with subsequent modifications of Bright & Bouchard 2008 and Alonso-Zarazaga et al. 2010; see also below). DNA data for *Trichalophus* are exceptionally scarce, with only four public partial CO1 sequences (>400 bp) of *T. alternatus* presently available from either Barcode of Life Database (BOLD) or GenBank.

LeConte (1876) established the genus for six nominal Nearctic species known to him, four of them having been described earlier as *Alophus* (*A. didymus*, *A. constrictus* LeConte, 1857, *A. alternatus*, *A. seriatus*) plus two newly described (*A. simplex*, *A. planirostris*). Six other currently valid Palaearctic species (Yunakov 2013) described prior to 1876 were added later; one of them was originally described as *Hypsonotus* Germar (*H. boeberi* Schoenherr, 1826) and five others as *Alophus* (*A. albonotatus* Motschulsky, 1869, *A. humeralis* Gebler, 1834, *A. lineatus* Gebler, 1841, *A. quadriguttatus* Gebler, 1829, *A. rudis* Boheman, 1842). After 1876, the Palaearctic part of the genus grew quickly in size. By the year 1915 *Trichalophus* included all but six of its 44 currently valid Palaearctic species-group taxa (Yunakov 2013). This notable increase was mainly due to the efforts of Johannes K.E. Faust and Edmund Reitter who, together with a few others, introduced 30 currently valid species-group names described from specimens collected on the Asian frontiers of the rapidly growing Russian Empire (Siberia, Russian Far East, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan, Mongolia, Xinjiang Uyghur Autonomous Region of China; Pierce 1960; Bajtenov 1974). Oddly enough, two new *Alophus* species, *A. caudiculatus* and *A. compressicauda*, were reported by Fairmaire (1886, 1887, respectively) from geographically distant Yunnan situated on the extreme southwest of China. The latter records, if indeed belonging to *Trichalophus*, would extend the genus' range for over 1,000 kilometers southwards. In 1913 Reitter described 13 species-group taxa in a key to all Palaearctic species known to him. Until now Reitter's revision has remained the most comprehensive single publication on *Trichalophus* weevils.

For the following hundred years the genus was neglected and only six new species-group names were introduced. Among them are both species recorded from Japan: *T. rubripes* Zherikhin & Nazarov, 1990 and *T. nutakkanus* Kôno, 1936; the former also found on the continent, while the latter is endemic to Hokkaido. Two other species were named from the mountains of the former Soviet Central Asia (*T. lixomorphus* Bajtenov, 1974 and *T. krauseanus* Bajtenov, 1975), while one (*T. korotyaevi* Zherikhin & Nazarov, 1990) was described from Sakha Republic (=Yakutia). Additionally, Suvorov (1915) established a monotypic genus *Pseudalophus* for his new species *P. tibetanus* described from an unknown number of syntypes collected during Pyotr K. Kozlov's (1863–1935) Mongol-

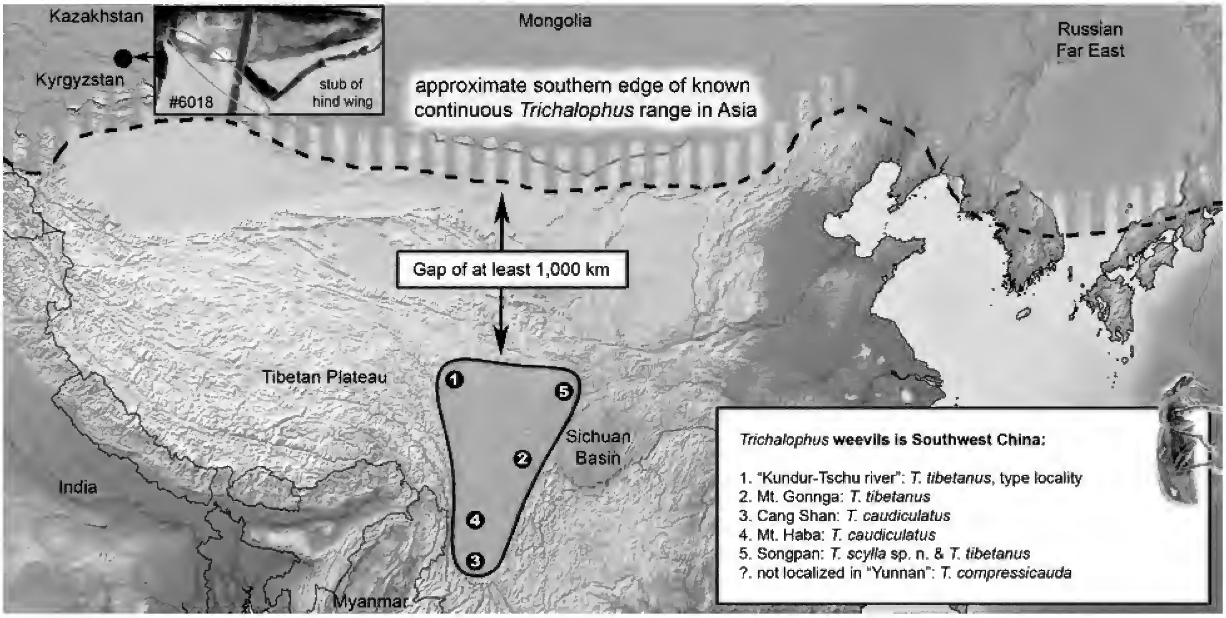

Fig. 1. Known geographic distribution of *Trichalophus* is Southwest China. Inserted image of female specimen #6018 from Kazakhstan shows hind wing brachyptery in *Trichalophus*.

Tibetan expeditions 1899–1901. The published temporal and geographical data of this species are identical with those of *Notaris kozlovi* Korotyaev, 1979 (Grebennikov & Kolov, unpublished) and the type locality is in the present day extreme northwest of Sichuan (Fig. 1). The four-line description of the new genus hinged on two characters distinguishing it from "*Alophus*", namely (a.) elytra strongly compressed "internally" (i.e. as if a force was applied in the horizontal plane therefore flattening elytra in the vertical plane) and (b.) elytral surface "naked" (= lacking vestiture). The former character is known to occur in Palaearctic *Trichalophus* and was used by Fairmaire (1887) to derive the name *compressicauda* for a species from nearby Yunnan, while the latter character might perhaps be attributed to abrading. Suvorov's original description was suggestive of a *Trichalophus* species, and, not surprisingly, Yunakov (2013) synonymized both generic names.

This project began on May 19, 2010, when the first two *Trichalophus* specimens (#0713 & #0714, Figs 3, 5), among those reported below were found under stones in the alpine zone of the Cang Shan Mountain Range in Yunnan (Fig. 1). The find was most inspiring and seemingly supportive of Fairmaire's historical claim that the genus was present so far south. During the next two years additional specimens were recovered in the same and three other high altitude localities in Yunnan (Mount Haba) and Sichuan (Mount Gongga and Songpan, the latter seemingly supporting two sympatric species). Phenetic similarities and subsequent analysis of DNA barcodes suggested that those were indeed species of *Trichalophus*. The wide gap seemingly separating these *Trichalophus* of Southwest China from their congeners in the north (Fig. 1) became partly bridged when the former "*Pseudalophus*" *tibetanus* was transferred to *Trichalophus* (Yunakov 2013). At that stage it became evident that *Trichalophus* was indeed present in Yunnan and Sichuan. The discovery of the high-altitude and the extreme southern representatives of a widely distributed trans-Beringian genus suggests a refugial distribution since the last glacial period (Darwin, 1859: 373–382). The goals of the present paper, therefore, are (1.) to attempt unfolding the evolutionary past of the newly sampled *Trichalophus* specimens from Southwest China using mainly mtDNA data and (2.) to report these findings in the framework of ranked Linnaean classification. Additionally, an attempt is made to provide an illustrated overview of all ten extant genera of Alophini and, therefore, to bring attention to this poorly defined, and taxonomically disorganized weevil tribe.

MATERIAL AND METHODS

Museum abbreviations, followed by the curator's name:

CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (P. Bouchard)
IZCAS Institute of Zoology, Chinese Academy of Science, Beijing, P.R. China (R. Zhang)
MNHN Muséum National d'Histoire Naturelle, Paris, France (H. Perrin, A. Mantilleri)

Fig. 2. Habitats of *Trichalophus* spp. in Southwest China. A–C: *T. scylla* sp. n., Songpan, Sichuan; D–F: *T. tibetanus*, Songpan, Sichuan; G–I: *T. caudiculatus*, Cang Shan, Yunnan; J–L: *T. caudiculatus*, Mt. Haba, Yunnan.

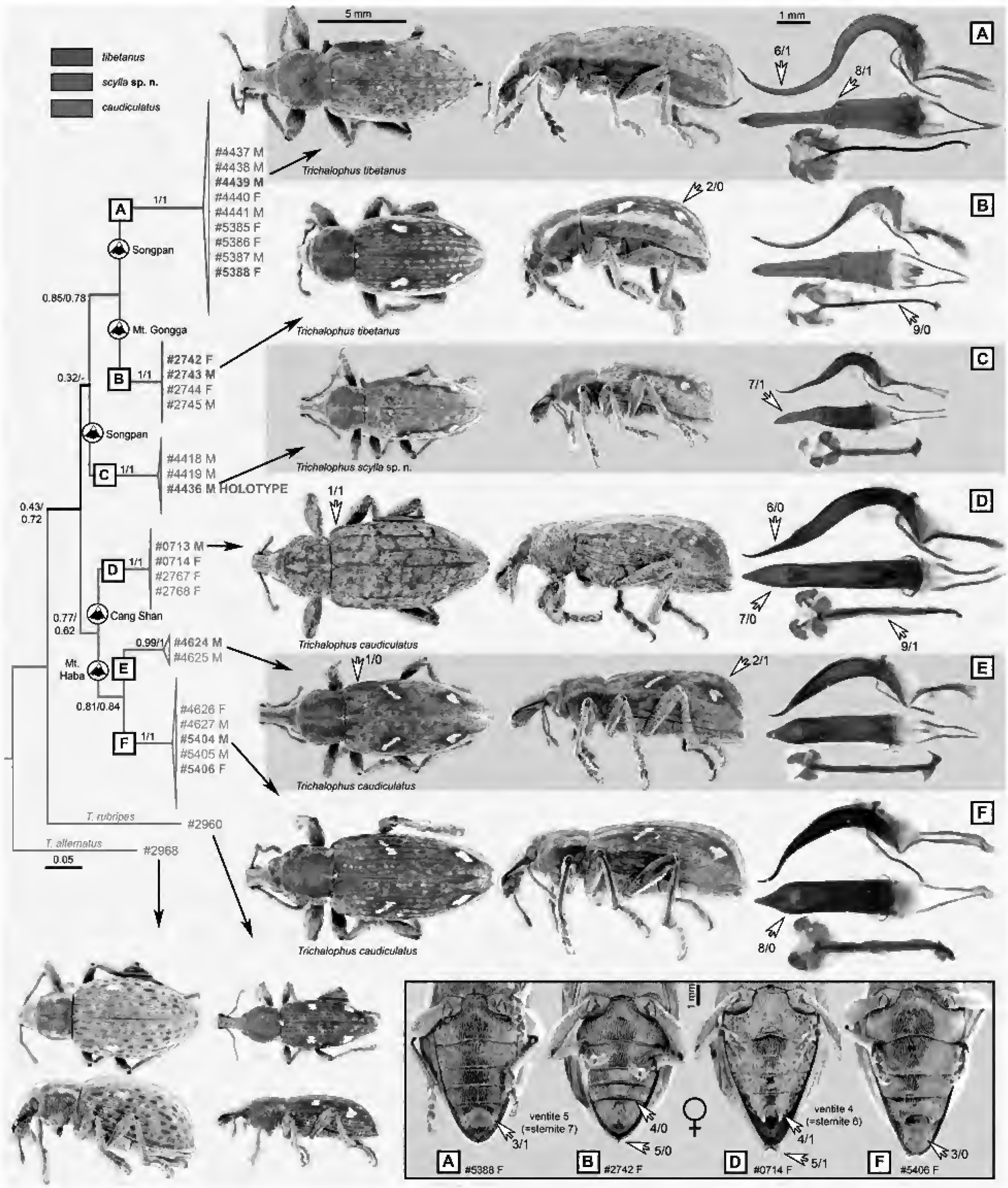

Fig. 3. Maximum Likelihood inference phylogram of *Trichalophus* weevils from Southwest China using the 658 bp of the mtDNA barcoding CO1 gene fragment. The tree is rooted on *Graptus circassicus* (Entiminae: Alophini; not shown); two extraterritorial outgroup *Trichalophus* (#2960 & #2968) are in grey. Digits at internodes are ML/MP bootstrap values. Six geographical evolutionary groups of *Trichalophus* are marked as clades A–F in white squares; note that Mount Haba and Songpan each harbours two evolutionary groups. Black long arrows link respective terminal clades with an image of their representative. Specimen numbers in bold are those of imaged males (M, to the left of the tree) or females (F, in the insert showing ventral view). Black and white short arrows indicate morphological characters and, after a slash, their states (Table 1).

MTD Senckenberg Naturhistorische Sammlungen, Dresden, Germany (K.-D. Klass, O. Jäger)
ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (B.A. Korotyaev)

The length of the body was measured in dorsal aspect from the elytral apex to the anterior edge of the pronotum. Distribution map (Fig. 1) is generated using the on-line SimpleMappr tool (Shorthouse 2010). The chronostratigraphic timing follows Cohen et al. (2013). Nomenclature of male genitalia follows that of Wanat (2007). The term "Southwest China" is delimited to two Chinese provinces, Yunnan and Sichuan. The term "base pair" is abbreviated as bp when referring to sequence length; abbreviations "syn. n" and "sp. n." denote new synonym and new species, respectively.

Specimen sampling, handling and gathering DNA data

Except for two specimens #4418 and #4419 sifted from *Rhododendron* L. leaf litter, all newly collected *Trichalophus* were handpicked from under stones (Figs 2A–L) in the alpine zone (Fig. 2J), or on a glade in the upper forest zone (Fig. 2D) in Southwest China. In total 38 adult *Trichalophus* beetles were collected in the following four localities (Fig. 1; in brackets are the total number of specimens followed after a slash by the number of those successfully sequenced for DNA barcode >400 bp): the Cang Shan Mountain Range (4/4), Mount Haba (12/7), Mount Gongga (4/4), and the vicinity of Songpan township (18/12). A leg was removed from a specimen for DNA extraction. All specimens used for DNA barcoding have at least one unique identifier label with the code CNCCOLVG0000XXXX; this format is shortened to the last four digits #XXXX when a specimen is referred to (Figs 3, 4). Specimen images, geographical data, primers, original electropherograms and other relevant data pertaining to all 35 matrix-forming sequences can be seen online in the publicly accessible dataset "*Trichalophus* 35 [DS-TRICHAL]" on the Barcode of Life Database portal (doi: dx.doi.org/10.5883/DS-TRICHAL). Genitalia of six males each representing a terminal cluster (=evolutionary group) as detected in the phylogenetic analyses (see below) were dissected, imaged (Fig. 3) and stored in microvials with glycerol pinned with the specimens.

DNA analyses and matrix construction

Three separate DNA analyses were performed. The **Maximum Likelihood** (ML) and the **Maximum Parsimony** (MP) analyses attempted to place the diversity of

Table 1. Discrete morphological characters for diagnostics of *Trichalophus* weevils in Southwest China (Fig. 3)

1. Elytral shoulders and elytral sides in basal 2/3, dorsal view: shoulders rounded, sides evenly widening posterad (0); shoulders angular, sides subparallel (1).
2. Elytral dorsal and posterior profile (=declivity), lateral view: evenly and gently rounded throughout (0); flattened dorsally and abruptly curved (1).
3. Female, ventrite 5, bumps and depressions on surface, ventral view: absent (0); present (1).
4. Female, ventrite 4, two sharp points at posterior edge, ventral view: absent (0); present (1).
5. Female, posterior projections of elytral apices, ventral view: absent (0); present (1).
6. Male genitalia, long, thin, and curved apical lamella of aedeagus (lateral view): absent (0); present (1).
7. Male genitalia, aedeagus, dorsal view: symmetrical (0); asymmetrical (1).
8. Male genitalia, aedeagus, notch in lateral outline, dorsal view: absent (0); present (1).
9. Male genitalia, sternal apodeme 9, dorsal view: thin (0); thick (1).

clade	species	Locality	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
A	*tibetanus*	Songpan	0	0	0	1	0	1	0	1	0
B	*tibetanus*	Mt. Gongga	0	0	0	1	0	1	0	1	0
C	*scylla* sp. n.	Songpan	0	0	?	?	?	0	1	0	1
D	*caudiculatus*	Cang Shan	1	1	1	0	1	0	0	0	1
E	*caudiculatus*	Mt. Haba	0	1	?	?	?	0	0	0	1
F	*caudiculatus*	Mt. Haba	0	1	1	0	1	0	0	0	1

Trichalophus from Southwest China into phylogenetic and geographical perspective. Both ML and MP used the same matrix of 35 DNA barcodes with a minimum and maximum length of 400 bp and 658 bp, respectively. The ingroup consisted of 27 *Trichalophus* specimens from Southwest China, while the outgroup included two extraterritorial *Trichalophus* specimens representing *T. rubripes* from the Russian Far East and *T. alternatus* from Canada (Fig. 3). The rest of the outgroup was formed by six specimens of *Graptus circassicus* Solari, 1945 from Georgia: Abkhazia. Both ML and MP analyses were implemented using MEGA 6 (Tamura et al. 2013), including (a.) topology building, (b.) statistical support test by using 1000 repetitions of bootstrapping and (c.) search for the best substitution model for ML analysis (T92+G). The root was consistently placed between *Graptus* and *Trichalophus*. The GenBank accessions for these 35 sequences are KM538655–86, KJ445708, KJ445709, KJ445712; all of them are new, except for the three latter *Graptus* sequences.

The third DNA analysis was performed to date the ingroup branching events and to re-test the phylogenies suggested by the ML and MP analysis. The original matrix of 35 sequences was reduced to include only 23 full-length DNA barcodes (658 nt; except for the sequence of *T. alternatus* with 609 bp). The second analysis was performed in BEAST v1.8.0 (Drummond et al. 2012) utilizing the Bayesian inference (BI) approach with no *a priori* grouping, all default priors and options, GRT+G+I nucleotide substitution model (instead of the T92+G+I not offered in the software; the latter model was detected in a separate model-searching analysis in MEGA 6 as having the best fit), strict linear molecular clock and nucleotide substitution rate of 0.018 (Papadopoulou et al. 2010). Tracer 1.6 (Rambaut et al., 2014) was used to graphically determine stationarity and to check convergence of runs. The "burn in" option was implemented eliminating the first 2500 of the 10000 obtained trees. The resulting topologies from each of three analyses (ML, MP, BI) were visualized in FigTree v1.4 (Rambaut et al. 2014).

Contribution from morphology

Morphological data are not expected to contribute decisively in DNA-dominated phylogenetic analysis, particularly in shallow branches of the tree of life (Ward 2011) conventionally called "species" in ranked classification (Hey 2001). Consequently, no effort was made to merge the DNA matrix with a few morphological characters scored for the ingroup (Table 1). Instead, DNA-determined *Trichalophus* clusters (= evolutionary groups by Hey 2001 or *clades A-F* on Fig. 1) were *a posteriori* scrutinized in search of diagnostic morphological characters (Maddison 2014), not necessarily synapomorphic (Ward 2011). The easily observable dorsal color pattern, being either too variable or subject to abrasion, was judged as unreliable for diagnostic purposes in *Trichalophus*. An additional effort was made to explore structures of male genitalia by dissecting a single male per each of six clades detected on the phylogenetic tree (Fig. 3).

Integrating molecular phylogenetic results into taxonomy

In biodiversity studies taxa are normally named first and then their phylogeny and boundaries are analysed, if ever. This approach, although logically awkward, has strong historical roots from the times when (a.) phylogenetic theory was not practiced by taxonomists, and (b.) researchers lacked adequate data to perform sufficiently detailed analyses when naming their new species. Advent of Hennigian principles coupled with availability of DNA sequences challenges this classical and logically deficient approach (Ward 2011). A modern student of biodiversity is expected to (A.) delimit evolutionary groups through a formal analysis, then (B.) make a balanced, responsible and subjective judgement using all available evidence sources as to which clades need names (Hey 2001) and then (C.) conservatively apply formal names, either pre-existing or newly proposed. In other words whenever possible, taxa naming should not be done before but after the analysis and discussion, not to abuse logic by putting the cart before the horse. Through most of the present paper all six tree-delimited clades representing candidate species (Fig. 3) are referred to by using informal non-taxonomic names (*clades A-F*, italicized). Therefore, the taxonomic part of this paper using three valid species-group names (two previously used and one new) and synonymizing one name follows the Results section and most of the Discussion.

RESULTS

The Maximum Likelihood (ML) analysis produced the best tree (Fig. 3) with the highest log likelihood of –3265.92. All *Trichalophus* specimens from Southwest China formed a weakly supported clade with highly resolved internal structure consisting of six *clades A–F*. The Maximum Parsimony (MP) analysis resulted in seven best trees (length: 558, consistency index: 0.64, retention index: 0.90; topologies are not shown) also recovering the same six *clades A–F* (as in Fig. 3). In both analyses the ingroup was recovered as a clade. The only backbone topological difference of the MP strict consensus tree (as compared to the ML topology, Fig. 3) was that the *clade C* was recovered as the sister to the rest of *Trichalophus* from Southwest China.

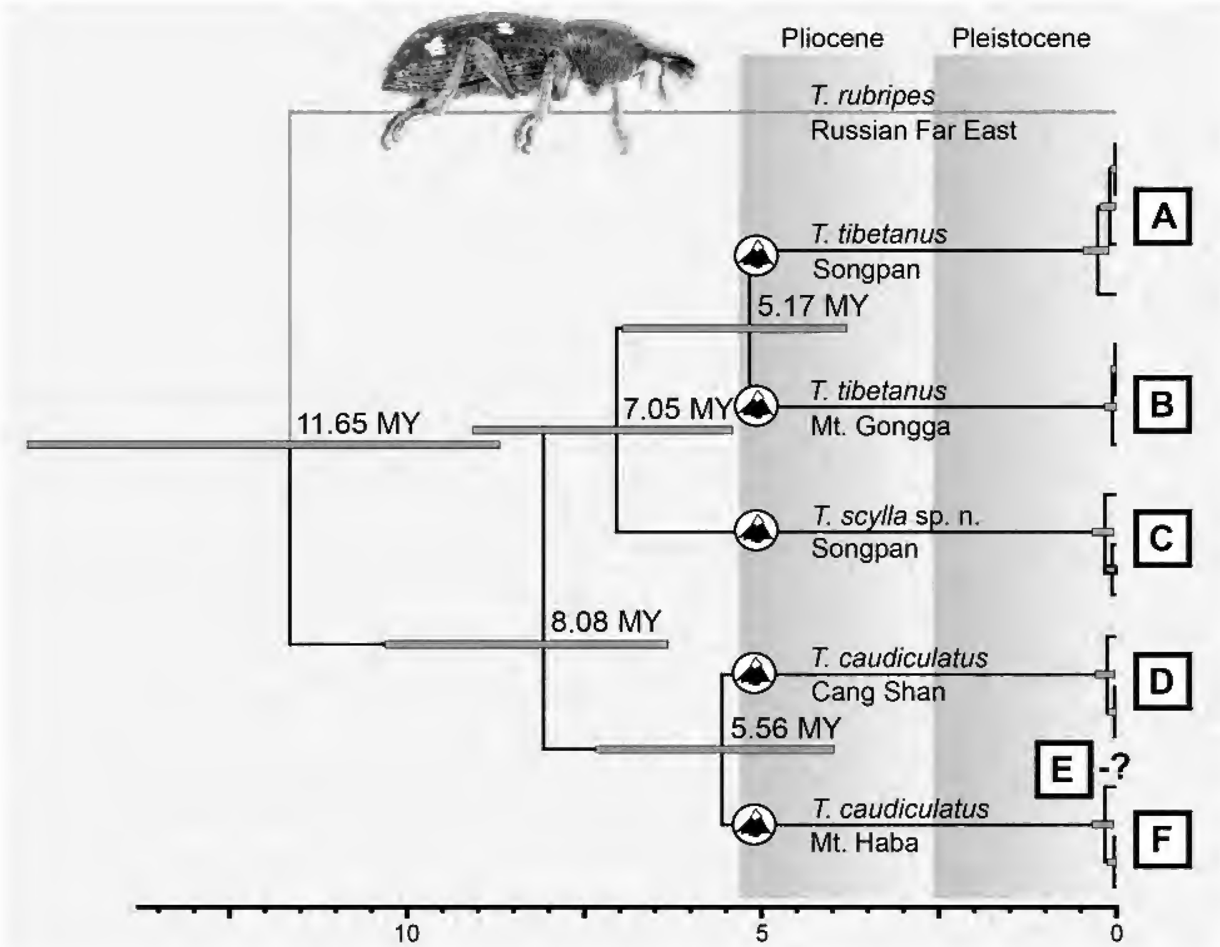

Fig. 4. Ultrametric tree dating evolutionary events of *Trichalophus* beetles in Southwest China. Digits at nodes and on the scale below are million years before present. Node bars represent 95% confidence intervals of the age estimate.

Temporal analysis in BEAST (Fig. 4) recovered all *Trichalophus* specimens from Southwest China in a clade with the same internal backbone topology as in the ML analysis (Fig. 3, although some specimens and the entire *clade E* were not represented in the BEAST analysis due to inadequate sequence length). The inferred timing of the origin of the Southwest China *Trichalophus* is 11.65 MY, while the clade's diversification leading to the five *clades A–D* and *clade F* range between 8.08 MY and 5.17 MY (Fig. 4).

DISCUSSION

mtDNA phylogeny and phylogeography of *Trichalophus* in Southwest China

Recovery of a monophyletic *Trichalophus* radiation in Southwest China (Figs 3, 4) should be treated with caution, since limitations in the number of the in- and out-group representatives did not permit a rigorous test. Little other evidence is available to challenge this hypothesis. The entire *clade A-F* has a compact range allopatric to that of the rest of the genus (Fig. 1), although the disjunct distribution might be plausibly attributed to the lack of adequate sampling effort to bridge the gap. Morphologically *Trichalophus* beetles from Southwest China are seemingly large-bodied compared to other two species (Fig. 3), although adding more *Trichalophus* in the analysis might challenge this pattern. Nearly all of the ingroup morphological characters (Table 1) cannot be adequately matched with those for the rest of the genus due to the lack of comparative data. Summing up, compact distribution (Fig. 1) of monophyletic *Trichalophus* of Southwest China (Figs 3, 4) is a weakly supported hypothesis to be eventually retested. Internal structure of six ingroup clades (Fig. 3) is mainly consistent with limited geographical (Fig. 1) and morphological (Table 1) data and is further discussed when Linnaean species are delimited (see below).

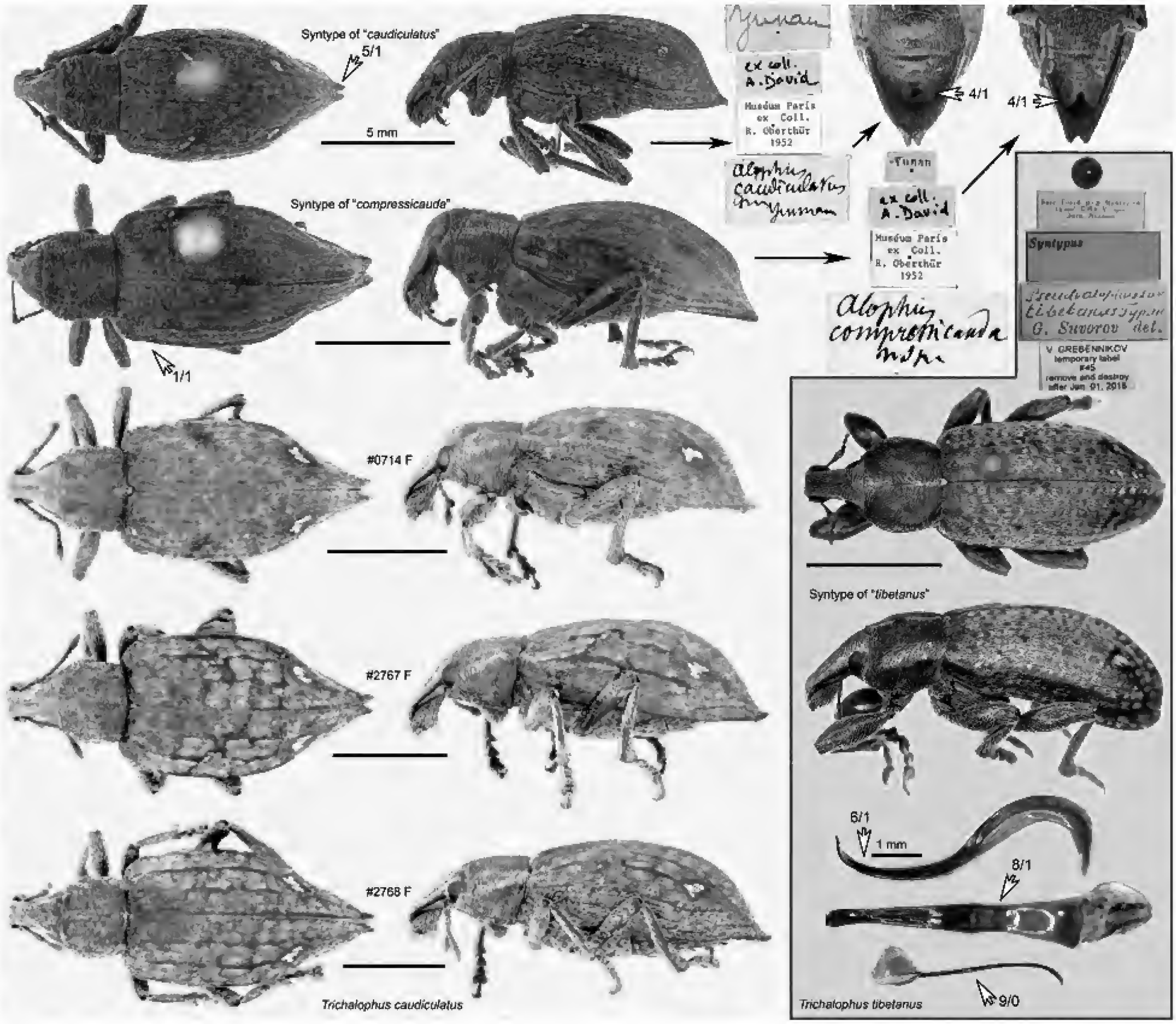

Fig. 5. Type specimens and original labels of three historical *Trichalophus* species names from Southwest China (*caudiculatus*, *compressicauda*, *tibetanus* currently assigned to two valid species *T. caudiculatus* and *T. tibetanus*), together with three *T. caudiculatus* females (#0714, #2767, #27678) sequenced for DNA barcode (Fig. 1). Black and white arrows indicate morphological characters and their states (Table 1, separated by a dash). Images of *caudiculatus* and *compressicauda* syntypes and their labels: Antoine Mantilleri, © MNHN.

Unlike at least some of its more northern congeners, *Trichalophus* in Southwest China inhabit high altitudes (3704–4158 m). Such a characteristic of the southern-most representatives of a temperate northern hemisphere clade of low-dispersing organisms is consistent with the basic Quaternary expansion-contraction model of latitudinal range change (Qiu et al. 2011). The latter stipulates extensive latitudinal range shifts in the form of southward movement during glacials followed by rapid expansions northwards during interglacials (Qiu et al. 2011). If so, distribution of *Trichalophus* in Southwest China (Fig. 1) is a direct result of the last warming following the Last Glacial Maximum (26,000–19,000 ybp). More specifically, the observed data are consistent with at least three sub-hypotheses (numbering after Qiu et al. 2011): (iii) long-term isolation and survival in multiple localized refugia (*clades A–D* and *clade E+F* in Fig. 3), (ii) population isolation and endemism due to river course dynamics (*clade D* versus *clade E+F*) and (iv) glacial *in situ* survival of some hardy alpine species on the Tibetan plateau itself (population of *T. tibetanus* represented by the type specimens, Fig. 5). Like the hypothesis on monophyly of *Trichalophus* in Southwest China, all phylogeographical inferences are highly preliminary due to material and data limitations.

With no suitable fossils to calibrate a *Trichalophus* molecular clock, the temporal aspect of *Trichalophus* evolution in Southwest China (Fig. 4) relies on the *a priori* mtD-

NA substitution rate of distantly related Tenebrionidae (Papadopoulou et al. 2010). The obtained dates of the *Trichalophus* cladogenesis (Fig. 4) are comparable to those of the sympatric and similarly high-altitude and flightless weevil genus *Niphadomimus* Zherikhin, 1987 (Grebennikov 2014a). Both agree that the lineage divergence took place well before the onset of the Pleistocene climate fluctuations. Both time estimations were based, however, on identical methods and substitution rates, which might have biased them both. Exact substitution rates may significantly vary depending on population size, founder effects, and a number of other less well-understood factors and, therefore, markedly differ from the assumed 0.018 substitutions per site per million years. In other words application of the user-friendly BEAST software and the obtained clear-cut dates (Fig. 4) should be treated carefully, since we are far from understanding the molecular clock (Lanfear et al. 2010), even for such relatively simplified and recent scenario as that of *Trichalophus* weevils in Southwest China.

Delimitation of Linnaean species for *Trichalophus* in Southwest China

The practical task of assigning Linnaean species names to the newly discovered *Trichalophus* from Southwest China, even with the help of a tree (Fig. 3), is far from being trivial. It involves at least one theoretical and two practical difficulties. First, imposing ranked classification on the continuum of the tree of life cannot be objectivised (Hey 2001; Ward 2011) and, therefore, involves arbitrary decisions (Sites & Marshall 2004). Second, despite sampling and analytical efforts, relatively little data on *Trichalophus* are available. For example, the relatively well-resolved DNA tree (Fig. 3) is that of a very short fragment of a fast-evolving mitochondrial maternally inherited gene and, therefore, only a proxy to organismal evolutionary history. Third difficulty is the existence of three available historical names, which have nomenclatorial priority and have to be interpreted and used, if considered as valid. These three issues have to be considered before the freshly sampled *Trichalophus* in Southwest China might be incorporated into the existing taxonomic scheme (Yunakov 2013). The first difficulty, concerning the issue of what a *Trichalophus* "species" is, will be resolved in this passage, while both practical issues are considered further below.

A "species" as a taxonomic category is purely and solely a label routinely and often inconsistently assigned to the shallow branches of the tree of life ever since Linnaeus. As such, "species" is no more real than other taxonomic categories like "genus", "family" or "phylum" (Hey 2001). Like every other taxonomic category, a "species" is a mere convenience required by the human mind to categorize and count biological diversity. Acceptance of this basic philosophical and methodological principle denies "species" reality in the same sense at it denies reality "genera" or other "higher" taxonomic categories. In practical terms a species is nothing more than a morphologically (or otherwise) diagnosable group of organisms preferably forming a clade and, most importantly, considered practically worthy of being called a species (Hey 2001). If to follow such an approach, decision on species boundaries almost fully rests with the revising author, which, in turn, results in the splitters versus lumpers issues, particularly in regard to a clade of allopatric populations. The authors normally feel free to either split them into as many species as possible, or lump them into a single one. The first approach is an example of unnecessary taxonomic inflation (Isaac et al. 2004) adding nothing but unnecessary names. The alternative lumping approach using a single species name and a geographic reference would label every allopatric evolutionary group equally well, while avoiding unnecessary additions to the already heavy nomenclatorial burden. Moreover, a scramble to call a "species" an allopatric evolutionary group, even if accompanied by correlating morphological and other differences, can be misleading when linked to the phenomenon of Sisyphean evolution (McKay & Zink 2014). Summing up, introduction of new species names should be done only when all alternative options have been shown as inadequate. Such a careful and reserved approach would not have created the multitude of meaningless and cryptic taxa (Riedel et al. 2013a, b; Vences et al. 2013).

Two among six terminal clades representing *Trichalophus* evolutionary groups (Fig. 3) are allopatric to all other ingroup clades (*clade B* and *clade D* from Mt. Gongga and Cang Shan, respectively). They should, therefore, be first assessed if each of them can be merged together with its strongly supported sister-group into a more inclusive clade to merit a species name. Indeed, *clade B* is strongly linked to the allopatric *clade A* (Fig. 3), so the *clade A+B* might itself be considered a candidate species. *Clade C* is recovered in the ML analysis as a sister to *clade A+B* (Fig. 3), but in MP analysis the sister group of *clade A+B* was the *clade D+E+F*. Remarkably, specimens of both *clade A* and *clade C* occur in sympatry in Songpan (or at least in parapatry; their two geographically closest samples were taken a few hundred meters apart). Moreover, while males and females of both *clade A* and *clade B* share all eight morphological character states (Table 1), their males differ in three genitalia characters from those of *clade C*. Such considerations strongly suggest that *clades A+B* and *clade C* (Fig. 3) should be treated as two separate species, respectively, and the former one as consisting of at least two geographically and morphologically unique evolutionary groups (*clade A* and *clade B*, Fig. 3). It is possible that in the future each *clade A* and *clade B* might be considered as separate species, but not until

the current nomenclatorial lumping arrangement is refuted as impractical.

The *clade D+E+F* emerges as the third and the last one to be designated as a Linnaean species among those represented in the ingroup (Fig. 3). Remarkably, *clade E* and *clade F* from Mount Haba, although genetically distinct, are formed by morphologically and geographically indistinguishable specimens (Fig. 3). This notable genetic dimorphism accompanied by full sympatry and morphological similarity is perhaps linked to incomplete lineage sorting (Funk & Omland 2003). The *clade E+F* is strongly supported as a sister to the geographically closest *clade D* and both share all but one morphological character (Table 1). Like the *clade A+B*, the *clade D+E+F* (Fig. 3) might also later require two Linnaean species, but not before the present conservative nomenclatorial decision is shown as inadequate.

Matching historical names with the tree-delimited *Trichalophus* Linnaean species

The most significant practical constraint is how to link three clades delimited for designation as Linnaean species (*clade A+B*, *clade C* and *clade D+E+F*, Fig. 3) with three available historical names (*T. caudiculatus*, *T. compressicauda* and *T. tibetanus*). The type specimens of the latter are well preserved and available for study (Fig. 5). Matching the type specimens of three historical names with three evolutionary groups in Fig. 1 can be done using three sources of evidence: (a.) similarity in body shape and in male genitalia, (b.) geographical proximity and (c.) biological characteristics expressed through the altitude of the type locality. No attempt was made to extract DNA from the type specimens, mainly because they were judged too old to warrant an attempt.

Of the three historical names, only the type specimen of *T. tibetanus* has information available from all three sources. Its type locality can be traced precisely (Figs 1, 5), while habitus and shape of male genitalia of a syntype (Fig. 5) match most closely those of the *clade A+B* (Fig. 3). The name *T. tibetanus* is, therefore, used to designate the *clade A+B* (Fig. 1). Such matching is far less straightforward with the both Fairmaire's names.

The most significant uncertainty with both names *caudiculatus* and *compressicauda* is that their type localities are imprecise, originally given as "Yunnan". The years when the types were collected are also unknown. Only the younger of these two names, *compressicauda*, has the collector's name stated: Père Jean Marie Delavay (=Father Delavay). It seems, however, plausible that Father Delavay also collected the type series of *caudiculatus*. Even though Fairmaire cited Armand David (= Father David) as the type specimen source for species described together with *caudiculatus* in the 1886 paper, Father Delavay was likely the original collector of at least some of them, since Fairmaire in the same paper also named *Cicindela delavayi* Fairmaire, 1886 in his honour. Indeed, the years before both species were described (1886, 1887) correspond with Delavay's second stay in China (1882–1891) (Anonymous 2014). This trip took place after Father Delavay's meeting with Father David in 1881, the latter convincing the former to collect specimens for the Muséum national d'histoire naturelle (Anonymous 2014). During his second stay in China, Delavay was mainly based in a Yunnan village somewhere between Lake Erhai and Lijiang township given as "Dapingzi" (Anonymous 2014). Delavay had two favourite climbing spots nearby: "Mount Heishanmen" (or "Ma'an Shan", west of "Dapingzi", see Handel-Mazzetti 2014; not definitely located, but distinct from the Cang Shan Mountain Range) and the Cang Shan Mountain Range along the western shore of lake Erhai (Lancaster 1993, Anonymous 2014). Besides these two high mountain localities, Father Delavay is definitely known to have collected in the alpine zone around Deqin in northwestern Yunnan, from where numerous alpine *Carabus* were sampled (T. Deuve, personal communication). It is highly probable that Father Delavay visited many other alpine localities in Yunnan, however those three were apparently most frequently visited and/or sampled for high altitude beetles.

Both *caudiculatus* and *compressicauda* were described from an unknown number of syntypes. Curatorial searches in MNHN in 2014 revealed a single syntype for each for these names (Antoine Mantilleri, personal communication). Their syntype status is corroborated by the fact that both specimens bear original identification labels and, moreover, fully agree with relatively detailed descriptions of both nominal species (Antoine Mantilleri, personal communication). Both syntypes, although not dissected, appear to be females by possessing posterior projections on elytral apices (character 5/1, Fig. 5) and posterior projections of ventrites 4 (character 4/1, Fig. 5). These two syntype characters match with those of the female specimens from *clade D* (Fig. 3); the other being angular elytral shoulders and subparallel elytra in their basal 2/3 (Table 1). Specimens from *clade D* inhabit the Cang Shan Mountain Range, which was visited on many occasions by Father Delavay, including altitudes above 4,000m (Lancaster 1993). Both Fairmaire's names, therefore, represent the best fit for the Linnaean species represented on Fig. 3 by the *clade D+E+F*, which, in turn, suggests their synonymy proposed below.

Taxonomic overview of *Trichalophus* in Southwest China

Trichalophus LeConte, 1876

Type species: *Alophus didymus* LeConte, 1854, fixed by subsequent designation (Bright & Bouchard 2008: 57).

Trichalophus caudiculatus (Fairmaire, 1886)

(Figs 2, 3, 5)
caudiculatus Fairmaire 1886: 353 (*Alophus*)

Type locality. Yunnan.

Type specimens. Syntype (MNHN, Fig. 5), likely female, examined from images in Fig. 5, labels in Fig. 5. Described from unknown number of syntypes.

= *compressicauda* Fairmaire, 1887: 129 (*Alophus*) **syn. n.**

Type locality. Yunnan.

Type specimens. Syntype (MNHN, Fig. 5), likely female, examined from images in Fig. 5, labels in Fig. 5. Described from unknown number of syntypes.

Diagnosis. This species is recognized by presence of apical elytral projections in females (character 5/1, Fig. 3).

Intraspecific variation. GenBank accessions: KM538662, KM538665, KM538667–68, KM538670–71, KM538676–77, KM538681–82, KM538684. Length: 12.3–14.5 mm (Cang Shan), 11.1–11.8 mm (Mount Haba, *clade E*) and 11.4–14.5 mm (Mount Haba, *clade F*). Specimens from both sampled localities (Fig. 1) slightly differ in dorsal coloration, shape of elytral shoulders and arrangement of posterior projection on ventrite 4 of females (Fig. 3). Aedeagus of a single male known from the Cang Shan Mountain Range is less curved and more elongate, as compared to those of two males dissected from Mount Haba (Fig. 3), while female posterior projections on elytral apices of the Cang Shan specimens are noticeably longer than those from Mount Haba (Fig. 3).

Additional material examined. 16 exx in total: 2 exx #0713–0714 (CNC) "P.R. CHINA, Yunnan, E slope Cangshan at Dali, N25°39'54.7" E100°06'04.5", 19.v.2010, 3815m, turn rock, V.Grebennikov"; 2 exx #2767–2768 (CNC) "P.R. CHINA, Yunnan, Cang Shan at Dali, N25°39'51" E100°06'05", 04.vii.2011, 3815m, under stone, V.Grebennikov"; 12 exx #4623–4628, #5403–5406, #6207–6208 (CNC) "CHINA, Yunnan, Haba Shan, N27°20'51" E100°05'33", 27.vi.2012, 4158m, under rock, V. Grebennikov".

Distribution. This species is known from the Cang Shan Mountain range and nearby Mount Haba, both in Yunnan (Fig. 1). Elevation: 3815–4158 m.

Trichalophus scylla sp. n.

(Figs 2, 3)

Diagnosis. Specimens of this species are unique among known congeners in Southwest China by two characters: they are the smallest and possess asymmetrical aedeagus in dorsal view (character 7/1, Fig. 3).

Description. Holotype, male (Fig. 3). GenBank accession: KM538655. Length: 9.4 mm. Combination of other morphological characters as in Table 1.

Intraspecific variation. GenBank accessions: KM538656, KM538679. Length: 9.0–9.4 mm.

Material examined. Holotype (Fig. 3) male (IZCAS): #4436: "CHINA, Sichuan, 23km E Songpan, N32°38'07" E103°49'10", 24.v.2012, 3704m, under rock, V. Grebennikov". Paratypes (CNC): 2 males #4418 and #4419 "CHINA, Sichuan, 23km E Songpan, N32°37'38" E103°50'03", 26.v.2012, 3791m, sifting 09, V. Grebennikov".

Distribution. This species is known only from the type locality some 20 km E of Songpan, Sichuan (Fig. 1), where it is found sympatrically with *T. tibetanus*. Elevation: 3704–3791 m.

Etymology. The species epithet is the Latinized Greek mythical name of Scylla, one of the Nereids, transformed by Circe into a six-headed monster and who, together with its counterpart Charybdis, threatened Odysseus' crew on their return voyage from Troy to Ithaca; noun in apposition.

Trichalophus tibetanus (Suvorov, 1915)

(Figs 2, 3, 5)
tibetanus Suvorov 1915: 338 (*Pseudalophus*)

Type locality. China, basin of the Blue river (=the Yangtze), the Kundur-Tschu river, 13200'.

Type specimens. Syntype (ZIN, currently on loan in MTD, Fig. 5), male, dissected by Rüdiger Krause, labels as in Fig. 5. Described from unknown number of syntypes. Twenty other similar specimens collected together with the imaged syntype are also likely part of the type series; of them four specimens each have a golden circle as in Fig. 5.

Diagnosis. This species is best distinguished by the presence of elongate and curved apical labella of aedeagus (character 6/1, Fig. 3) and relatively thick apodeme of male sternite 9 (character 9/0, Fig. 3).

Intraspecific variation. GenBank accessions: KM538657, KM538658, KM538659, KM538661, KM538663–64, KM538672–75, KM538680, KM538685–86. Length: 11.5–13.3 mm (Songpan) and 10.3–12.1 mm (Mount Gongga). Each elytron with single indistinct apical spot (Fig. 5), two indistinct spots, or two distinct spots (Fig. 3). Specimens from Mount Gongga have a long white longitudinal stripe laterally on each elytron (Fig. 3).

Additional material examined. 19 exx in total: 4 exx #2742–2745 (CNC) "P.R. CHINA, Sichuan, NE slope Gongga Shan, N25°53'53" E102°01'49", 8.vi.2011, 4085m, under stone, V.Grebennikov"; 15 exx #4437–4441, #5385–5388 and six not numbered specimens in ethanol (CNC) "CHINA, Sichuan, 23km E Songpan, N32°38'07" E103°49'10", 24.v.2012, 3704m, under rock, V. Grebennikov".

Distribution. Besides the type locality in the extreme north-western Sichuan, this species is also known from Mount Gongga and from vicinities of Songpan, both in Sichuan (Fig. 1); in the latter locality this species is found sympatrically with *T. scylla* sp. n. Elevation: 3704–4085 m.

Generic overview of the tribe Alophini

The proposed amalgamation of Alophini (as delimited below) with the tribe Tropiphorini (*sensu* Alonso-Zarazaga & Lyal 1999) by Zherikhin & Egorov (1991), for which a synonymous name Leptopiini was used by Marvaldi et al. (2014), is not followed here. Neither taxonomic arrangement was phylogenetically tested, therefore none is better than the other. Additionally, dissolving the compact and predominantly Holarctic Alophini in the much larger cosmopolitan Tropiphorini would discourage any practical effort to shed light on the genera involved, as attempted below.

The tribe Alophini was first proposed by LeConte (1876: 115) to incorporate the Palaearctic species grouped then in *Alophus* Schoenherr and species belonging to six Nearctic genera, five of them newly established: *Triglyphus* LeConte, *Plinthodes* LeConte, *Acmaegenius* LeConte, *Trichalophus* LeConte, *Lophalophus* LeConte and *Lepidophorus* Kirby, 1837. By the end of the millennium the tribe consisted of 15 valid genera, including three described from the Oligocene of the USA (*Centron* Scudder, 1893, *Geralophus* Scudder, 1893 and *Limalophus* Schudder, 1893, see Alonso-Zarazaga & Lyal 1999). Since then Bright & Bouchard (2008) synonymised the genus *Acmaegenius* under *Trichalophus* and reviewed the Alophini of Canada and Alaska. Alonso-Zarazaga et al. (2010) demonstrated that the sole known specimen of the monotypic genus *Ctenolobus* Desbrochers des Loges, 1892 from Morocco is conspecific with the type species of the otherwise strictly South American genus *Strangaliodes* Schoenherr, 1842 (Tropiphorini). As a result, *Strangaliodes* was transferred to the otherwise strictly Palaearctic Alophini and was keyed out against three other Mediterranean genera: *Graptus*, *Rhytideres* and *Seidlitzia* (Alonso-Zarazaga et al. 2010). Finally, Yunakov (2013) synonymized *Pseudalophus* under *Trichalophus*. At present the following 10 extant genera constitute the tribe Alophini:

***Graptus* Schoenherr, 1823** (Figs 6A, B) with 37 species-group taxa is distributed in Western Palaearctic (Yunakov 2013). Davidian & Arzanov (2004) revised and keyed 10 *Graptus* species from Russia and adjacent lands, including two newly described ones, and mentioned that many poorly known nominal species have been reported from the West Palaearctic.

***Lepidophorus* Kirby, 1837** (Figs 6C, D) consists of 11 brachypterous species found in western North America (Anderson 1997, 2012; Bright & Bouchard 2008), two of which, *L. inquinatus* Mannerheim, 1852 and *L. lineaticollis* Kirby, 1837, are also found on the Asian side of the Bering Strait (Yunakov 2013). Another extant North American species, *L. thulius* Kissinger, 1974, is known from numerous subfossil records on both side of the Bering Strait and, therefore, extant populations might perhaps be discovered in the northern Pacific Asia (as *Vitatitus* Kissinger, 1974 in Egorov et al. 1996 and in Anderson 1997). Anderson (2002) mentions that the genus cannot be reliably distinguished from *Dirotognathus* Horn, 1876 (Tropiphorini *sensu* Alonso-Zarazaga & Lyal 1999), giving support to a notion to synonymize both tribes (Zherikhin & Egorov 1991; Marvaldi et al. 2014).

***Plinthodes* LeConte, 1876** (Figs 6E, F) consists of two North American species, *P. foveirostris* Chittenden, 1925 from Ohio, North Carolina, Tennessee and Virginia and *P. taeniatus* LeConte, 1857 from British Columbia, Washington and Oregon (Anderson 2002). Bright & Bouchard (2008) questioned the distinctness of this genus from *Trichalophus*.

***Pseudobarynotus* Desbrochers des Loges, 1891** (Fig. 8) contains a single mysterious species *P. laticeps* (Desbrochers des Loges, 1875) known only from the type series and described from "Pyrénés". The type series could have been mislabelled, while Kazakhstan was suggested as its true origin (Alonso-Zarazaga et Lyal 1999). The later possibility is not unlikely, since the depicted syntype (Fig. 8) resembles a species of *Trichalophus* and might perhaps be later demonstrated as such.

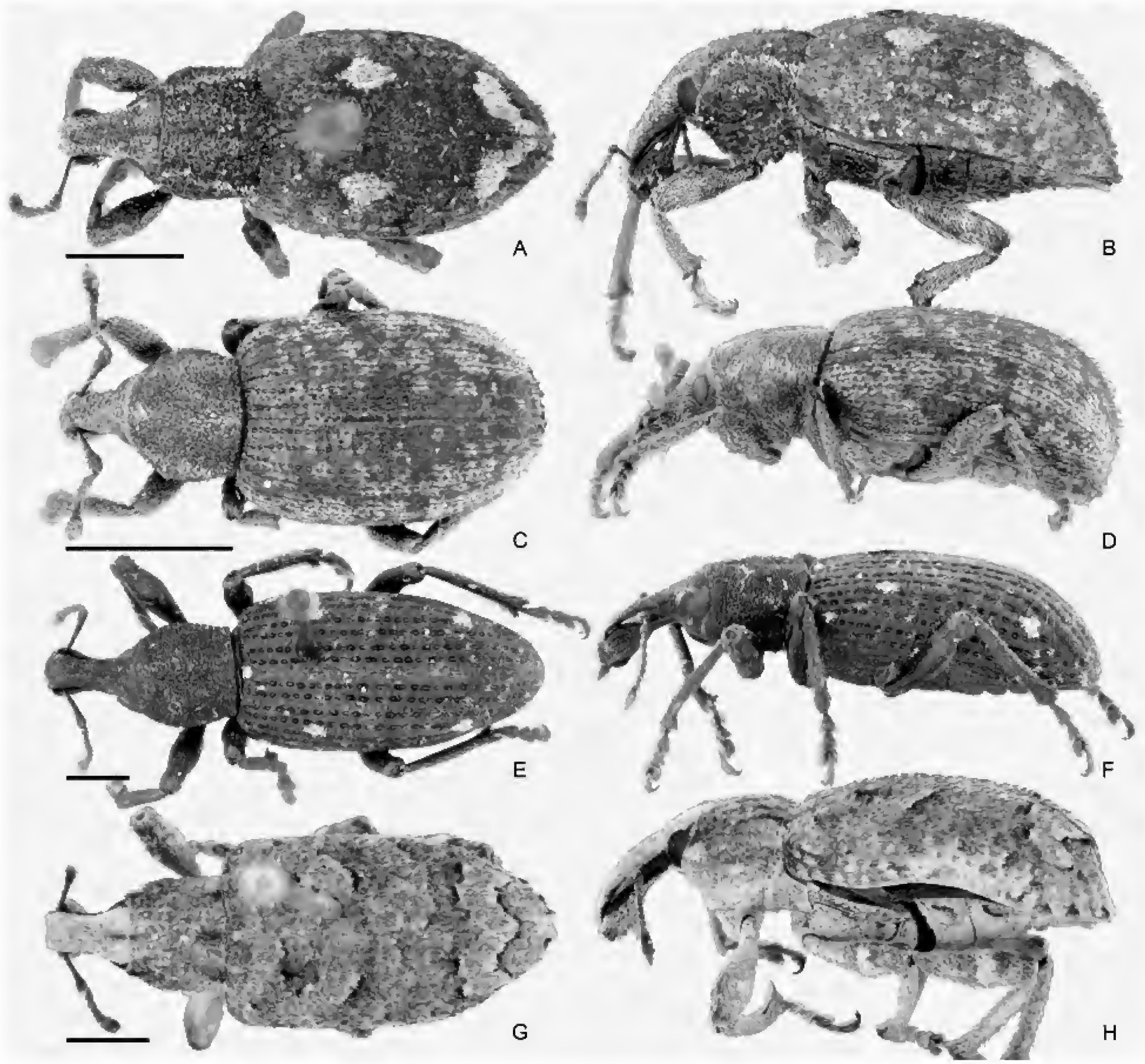

Fig. 6. Type species of the Alophini genera. A–B: *Graptus triguttatus* (Fabricius, 1775), Austria, Wien, date and collector unknown, CNC; C–D: *Lepidophorus lineaticollis* Kirby, 1837, USA, Alaska, Wasilla, 1.viii.1988, J.Pilny, CNC; E–F: *Plinthodes taeniatus* LeConte, 1857, Canada, British Columbia, Victoria, 6.vii.1962, B.Carr, CNC; G–H: *Rhytideres plicatus* (Oliver, 1790), no collecting data, CNC. Scale: 2 mm.

***Rhytideres* Schoenherr, 1823** (Figs 6G, H) includes three species widely distributed around the Mediterranean Sea (Yunakov 2013).

***Seidlitzia* Desbrochers des Loges, 1891** (Figs 7A, B) consists of two species and one non-nominal subspecies from Spain and Morocco (Yunakov 2013).

***Strangaliodes* Schoenherr, 1842** (habitus image in Alonso-Zarazaga et al. 2010, figs 1A, B) includes nine species from the South American Cordillera, all of them found in Chile and a few in neighbouring countries (Wibmer & O'Brien 1986); one of them also questionably recorded from Morocco (Alonso-Zarazaga et al. 2010). This is the only non-Palaearctic member of Alophini.

***Trichalophus* LeConte, 1876** (Figs 7C, D) consists of 51 species and one non-nominal subspecies distributed on both sides of the Bering Strait; for more details see the current paper.

***Triglyphulus* Cockerell, 1906** (Figs 7E, F) consists of two species, *T. ater* LeConte, 1876 and *T. nevadensis* Van Dyke, 1938 from the western part of the USA (Anderson 2002).

***Xeralophus* Korotyaev, 1992** (Figs 7G, H) was established to accommodate *Alophus cretaceus* Reitter, 1894, described from present day Ulan Bator, Mongolia. Besides

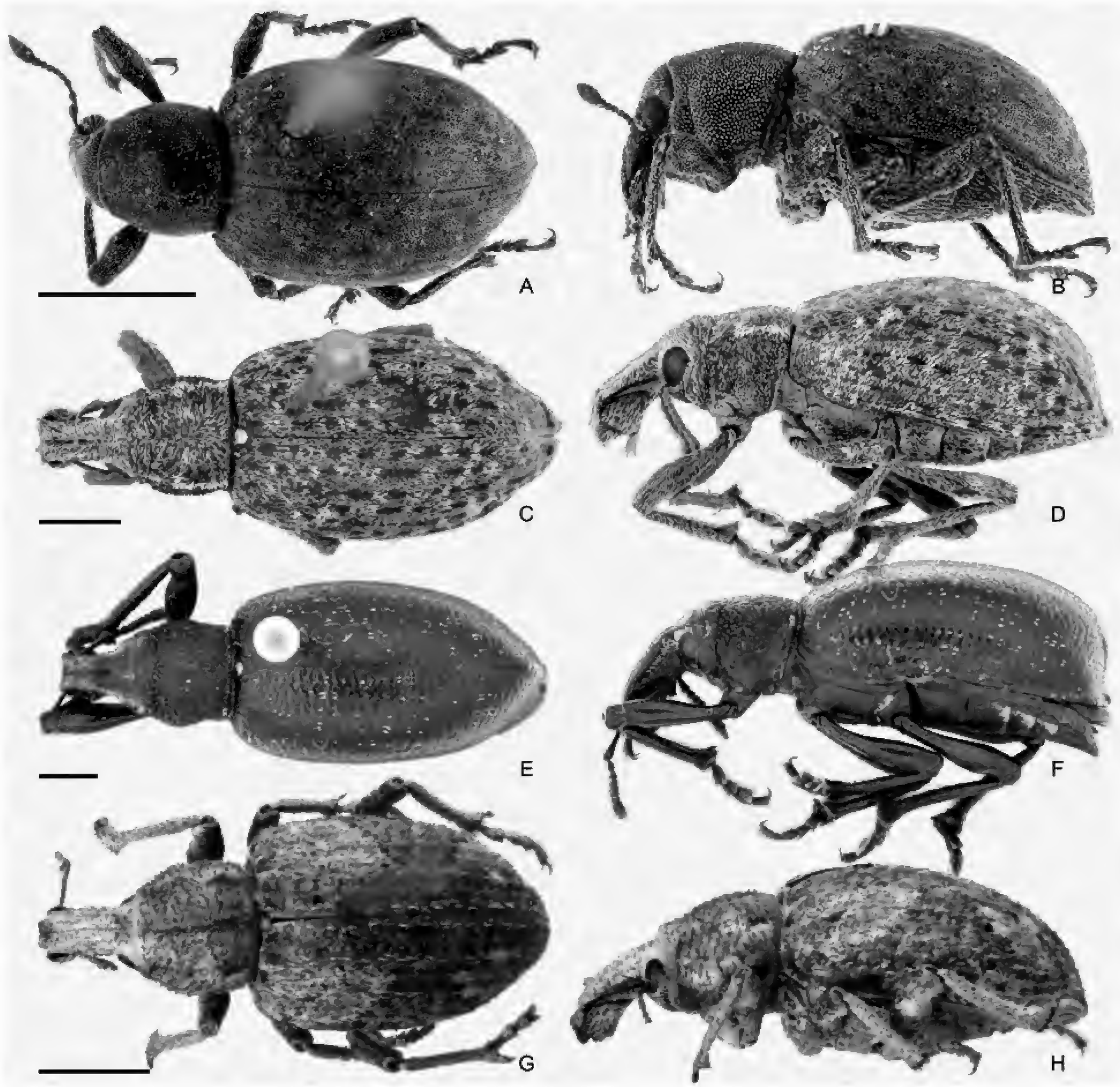

Fig. 7. Type species of the Alophini genera. A–B: *Seidlitzia maroccana* (Fairmaire, 1868), Morocco, date and collector unknown, MNHN, image: Antoine Mantilleri, © MNHN, original image showing right lateral view was digitally flipped horizontally to appear as left; C–D: *Trichalophus didymus* (LeConte, 1854), Canada, British Columbia, Kitsumkalum Lake, 16.vi.1960, B.S.Heming, CNC; E–F: *Triglyphulus ater* (LeConte, 1876), USA, Idaho, Bear, 26.vii.1977, B.Carr, CNC; G–H: *Xeralophus cretaceus* (Reitter, 1894), Russia, Tyva, Kyzyl, 6.v.1974, B.A.Korotyaev, ZIN, image: Andrey Frolov. Scale: 2 mm.

the type series, four more specimens were later reported, all found dead in sandy steppe of the neighbouring Tyva Republic of Russia (Korotyaev 1992). Korotyaev (1992) hypothesised that this xerophilic taxon is phylogenetically nested within the predominantly mesophilic "*Alophus*" (= *Graptus*). This hypothesis, if corroborated, would render the name *Xeralophus* a junior subjective synonym of *Graptus*.

CONCLUDING REMARKS

It seems worthy of reiterating some important and perhaps not too obvious generalities emerging from this study. First, if the genus *Trichalophus* does exist in the phylogenetic sense, then its presence has been reconfirmed in Southwest China for the first time since Suvorov (1915). Second, the last glacial retreat is likely responsible for the

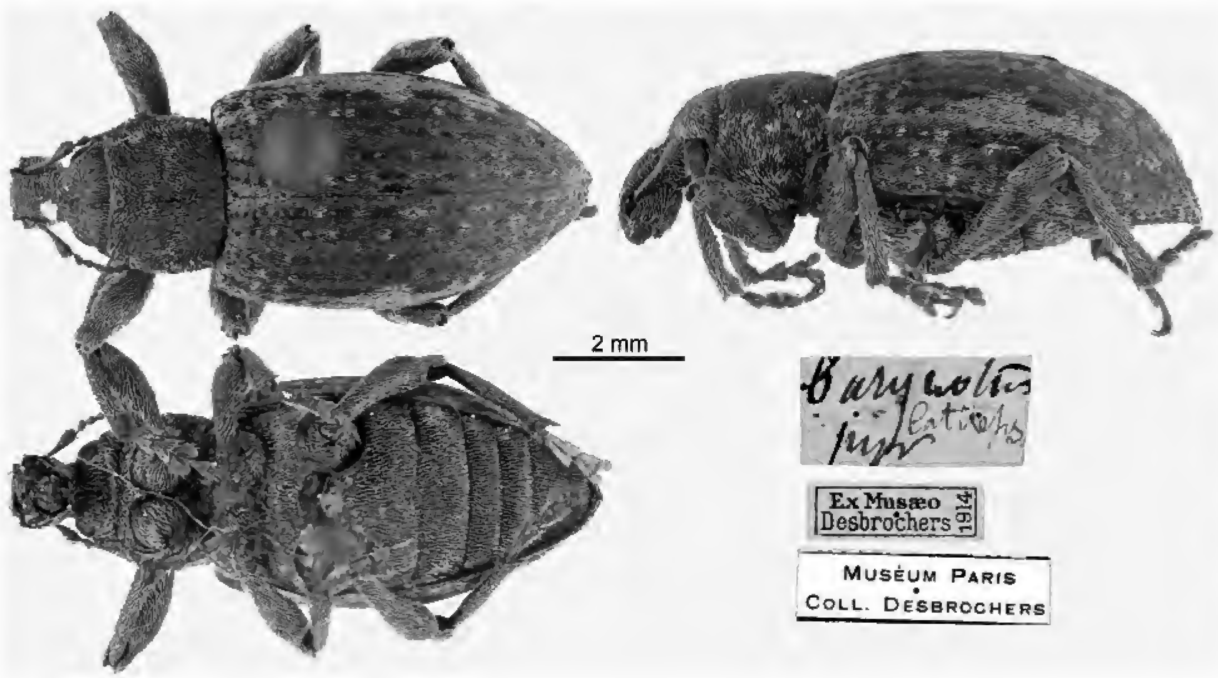

Fig. 8. *Pseudobarynotus laticeps* (Desbrochers, 1874), syntype, MNHN, image: Antoine Mantilleri, © MNHN.

present day high altitude presence of *Trichalophus* in the high mountains of Yunnan and Sichuan, but not for the diversification of the lineages leading to the extant populations. Third, in spite of the large body size and relative ease of sampling, *Trichalophus* is among the least understood genera of the Holarctic weevils. Such neglect is partly due to the abundance of ambiguous historical species names, particularly in Central Asia, which creates a nomenclatorial impediment and hinders further research. Fourth, relationships of *Trichalophus* in Alophini, and the overall phylogenetic validity of this tribe and most of its genera (particularly *Plinthodes*, *Pseudobarynotus* and *Xeralophus*) remain untested. When adequately studied, however, the genus *Trichalophus* is expected to be of significant biogeographic potential, similarly to other clades of low-dispersing organisms most suitable to reveal the geographical component on their evolutionary past (Murienne et al. 2014; Tänzler et al. 2014; Toussaint et al. 2015).

Acknowledgements. Curators of the collections mentioned above variously helped in accessing specimens under their care. Antoine Mantilleri (Paris, France) (1.) took syntype habitus and label images of both Fairmaire's names (Fig. 5); (2.) critically verified the match between both original descriptions and the imaged syntypes (Fig. 5) to help establish their name-bearing status and (3.) took images of *Barynotus laticeps* syntype (presently *Pseudobarynotus laticeps*) and of *Seidlitzia marrocana* syntypes (Figs 8 and 7A, B, respectively). Genrikh Ed. Davidian and Boris A. Korotyaev searched on my request for the ZIN specimen of *Xeralophus cretaceus*, which was imaged (Figs 7G, H.) by Andrey V. Frolov (all St. Petersburg, Russia). Thierry Deuve (Paris, France) advised on collecting sites of Father Delavay in Yunnan. David J. Clarke (Chicago, USA) collected and made available the sequenced specimen of *Trichalophus alternatus* (#2968). Ignacio Ribera (Barcelona, Spain) advised on implementation of DNA analytical techniques. Christian Schmidt, Eduard Jendek and Bruce D. Gill (all Ottawa, Canada) reviewed early versions of this paper.

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An annotated checklist of the inland fishes of Sulawesi

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Abstract. Sulawesi is the largest island of the Wallacea. Here, we present an annotated checklist of fish species recorded in Sulawesi's inland waters. We recognize a total of 226 species from 112 genera and 56 families. Gobiidae (41 species), Adrianichthyidae (20 species) and Telmatherinidae (19 species) are most species-rich, making up a total of 43% of the total species diversity. 65 species are endemic to Sulawesi's freshwaters, including 19 Tematherinidae, 17 Adrianichthyidae, and 17 Zenarchopteridae. 44% of the inland fish fauna are obligate freshwater fishes, followed by euryhaline (38%) and amphi-, ana- or diadromous (29%) taxa. 65 species have been recorded from lacustrine environments. However, we stress that the data available are not representative for the island's freshwater habitats. The fish species diversity of the spectacular lakes is largely explored, but the riverine ichthyofaunas are in clear need of further systematic exploration.

Keywords. Sulawesi, freshwater, fishes, endemism, Wallacea, SE-Asia

INTRODUCTION

Sulawesi is the largest island of the Wallacea, a biodiversity hotspot located between the Sunda and Sahul shelves (Mokodongan & Yamahira 2015, Myers et al. 2000, Whitten et al. 2002). The onset of the scientific investigation of Sulawesi´s inland waters and its fishes dates back to the late 19th century (Abendanon 1915a, b, Bleeker 1855a, 1858a, b, Boulenger 1897). Exploration of species diversity was, and still is, in the focus of ichthyological research on the island (e.g. Hadiaty 2007, Hadiaty & Wirjoatmodjo 2003, Hadiaty et al. 2004, Kottelat 1989a, b, c, 1990a, b, c, d, 1991, Larson 2001, Parenti 2008, 2011, Weber 1909, 1913), complemented more recently by studies on evolutionary biology (e.g. Herder & Schliewen 2010).

Sulawesi's freshwater environments are home to several endemic animal radiations that include gastropods, crustaceans, and fishes (e.g. de Bruyn et al. 2013, Herder et al. 2006a, Mokodongan & Yamahira 2015, Parenti 2011, Parenti et al. 2013, Rintelen et al. 2007a, b, Rintelen et al. 2012, Tweedley et al. 2013). Much of this diversity is restricted to species flocks confined to a few ancient lakes, systems that serve as models for the study of speciation processes (Herder & Schliewen 2010, Rintelen et al. 2010, 2012, Vaillant et al. 2011). Phylogeographic studies of the island's freshwater animals accordingly focused mostly on lineages of molluscs, shrimps, crabs, and fishes, with focus on the lake radiations (e.g. Mokodongan & Yamahira 2015, Rintelen et al. 2007b, 2014, but see also de Bruyn et al. 2012, 2013; reviewed by Rintelen et al. 2012).

Parenti recognized 57 species of freshwater fishes as endemic to Sulawesi, with the majority being restricted to the ancient lakes (Parenti 2011). Most of the non-endemic fish species are classified as secondary or peripheral freshwater fishes (Berra 2001), with occasional records of marine species (Kottelat 1990a, Tweedley et al. 2013).

Sulawesi´s lakes include some of the oldest lakes on earth. Lake Poso and the Malili Lakes in the highlands of Central Sulawesi are so-called ancient lakes, exceptionally long-lived lakes that have existed for more than 100,000 years (Brooks 1950, Rintelen et al. 2012). The Malili Lakes system is known for its endemic species flock of sailfin silversides (Telmatherinidae) (Herder et al. 2006a), but also includes small radiations of ricefishes (*Oryzias*) and gobies (*Mugilogobius*, *Glossogobius*; Hoese et al. 2015, Kottelat 1990d, Larson et al. 2014). Moreover, the lakes and their surroundings harbour endemic species of halfbeaks (*Dermogenys*, *Nomorhamphus*; Huylebrouck et al. 2012, Meisner 2001). Ricefishes (*Oryzias*, *Adrianichthys*) are the dominant fish radiation of Lake Poso (Kottelat 1990b). Remote lakes Lindu and Tiu are substantially smaller than the ancient lakes, and harbour two (Lindu) or one (Tiu) endemic (rice-) fish species (Mokodongan et al. 2014, Parenti 2008). Lake Tondano on the northern tip of North Sulawesi is the only known habitat of *Tondanichthys kottelati* (Collette 1995), an endemic genus and species of viviparous halfbeak (Collette 1995). Lake Tempe and Lake Sidereng are

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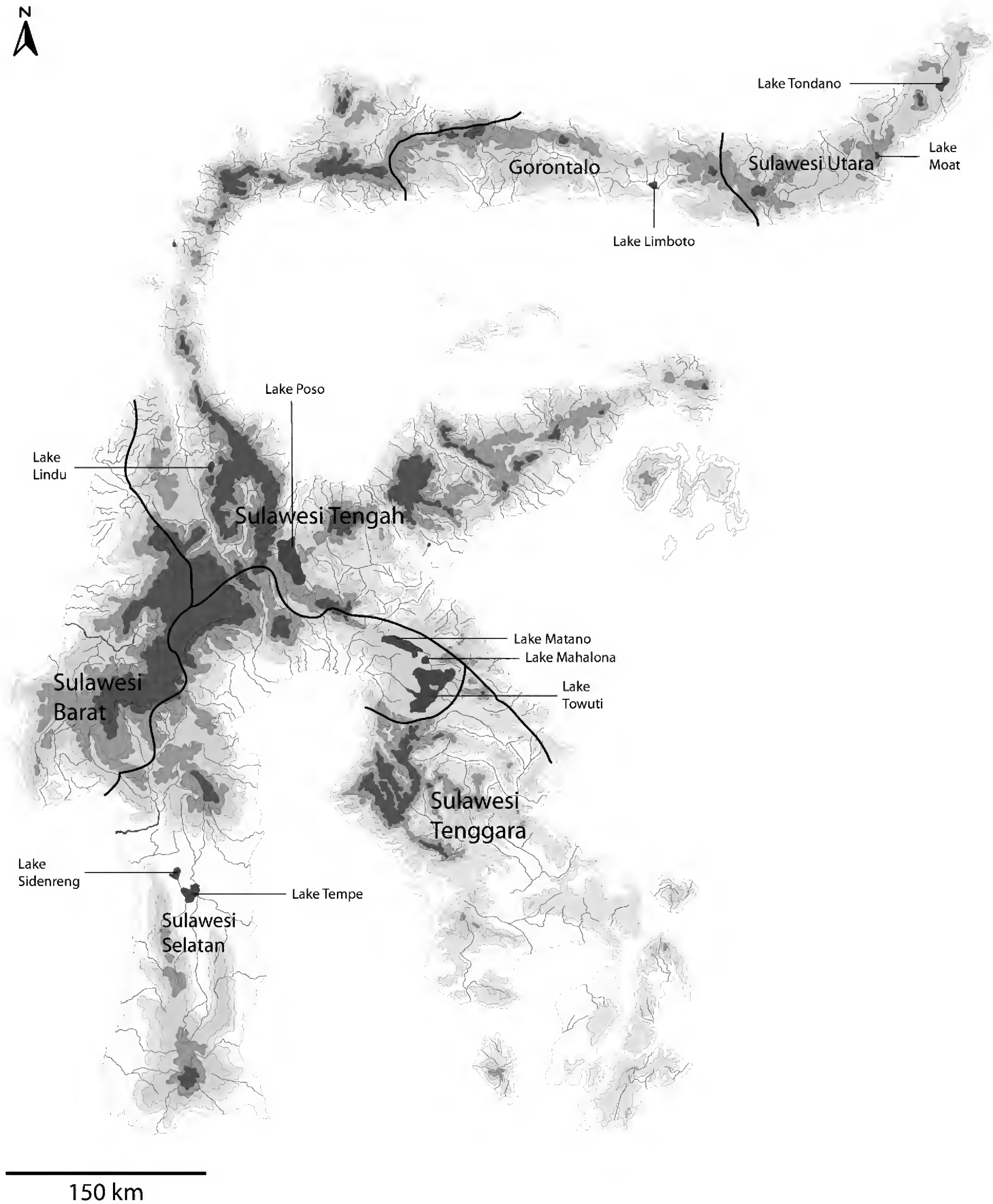

Fig. 1. Map of Sulawesi showing the island´s administrative partition as referred to in this study, major lakes are highlighted.

shallow lakes in southern Sulawesi, but little remains known about their fish fauna, and its present status apart from its use in aquaculture (Hadijah et al. 2014, Tamsil 2000) (for the location of Sulawesi´s lakes see Fig. 1).

In contrast to the ancient lakes, Sulawesi´s riverine fish fauna has attracted far less scientific interest, and the number of studies is limited (de Bruyn et al. 2013, Mokodongan & Yamahira 2015, Schwarzer et al. 2008, Tweedley et al. 2013). A typical feature of Sulawesi´s riverine environments is the absence of large, slow rivers and drainages (Kottelat 1990a), in contrast to the hydrology of most other larger Indonesian islands (Stelbrink et al. 2012). The majority of drainages are rather small and short, typically with medium to high stream velocity (Kottelat 1990a).

Sulawesi´s freshwaters have been subject to massive fish species introduction and alien species invasion (Herder et al. 2012a, Kottelat & Whitten 1996, Parenti 2011, Whitten et al. 1987). Alien fishes were introduced for food production (e.g. *Oreochromis* spp., *Channa* spp.) (Whitten et al. 1987), pest control (*Poecilia reticulata*), or aquarium trade (e.g. flowerhorn cichlids) (Herder et al. 2012a). The spread of populations of alien fish species in freshwater systems of the island is apparently rapid, and may pose as a threat to the native communities (e.g. Herder et al. 2012a, Tweedley et al. 2013).

Purpose of this paper

The literature on freshwater fish species of Sulawesi is complex and dispersed. The most recent comprehensive source covering the island's ichthyofauna dates back to 1993 (Kottelat et al. 1993), but is not focussed on the island's fishes, and meanwhile partially out-dated. Kottelat's recent catalogue on "The Fishes of the Inland Waters of Southeast Asia" (Kottelat 2013) includes Sulawesi, but focuses on the nomenclature of the whole Southeast Asian ichthyofauna, and the related bibliography. The present paper aims at summarizing ichthyological records from Sulawesi's inland waters. It provides an account of actual species records, and species that have not actually been recorded, but are likely to be present according to their known distribution. It is understood that the authors do not claim that this list is complete with respect to all records ever made, but aim at providing a baseline for analysing species records, required for upcoming investigations of the island's fauna.

MATERIAL AND METHODS

Literature records are compiled from the scientific literature; sources or records considered questionable were not included. Material examined was mostly collected during various field campaigns of the senior author´s group in Sulawesi, since 2002. Field methods applied during fieldwork include beach seining, dipnetting, gillnetting, scubadiving and electrofishing. Samples were either fixed in formalin (4%) prior to storage in ethanol (80%), or fixed and stored directly in pure ethanol (~98%). Specimens were determined to the lowest feasible taxonomical level using the most recent literature available. The systematic division largely follows Kottelat (2013). ZFMK: Fish collection of Zoologisches Forschungsmuseum Alexander Koenig Bonn, Germany. Coordinates with reference to ZFMK specimens are own species records, linked to the respective voucher. Records that are not linked to vouchers, represent visual records (F.H.); ZMH: Zoologisches Museum Hamburg in Hamburg, Germany; MZB: Museum Zoologicum Bogoriense in Cibinong, Indonesia.

Species occurrence is classified to: Euryhaline: species with a broad tolerance towards salinity and thus can be found in marine, brackish and freshwater environments (Hiroi & McCormick 2012); anadromous: species with adults entering marine environments and reproduction in freshwaters (Daverat et al. 2012); catadromous: species that migrate into marine environments for reproduction (Daverat et al. 2012); amphidromous: species that migrate between marine and freshwater environments for purposes other than reproduction (Daverat et al. 2012); freshwater: primary or secondary/obligate freshwater species with no marine stadium or life history phase (Berra 2001); introduced: non-native, introduced species.

Species expected to occur in Sulawesi, but lacking actual records from the island, are included as "potential", and justified. Clearly non-native species are classified as "introduced". Synonyms listed are restricted to the most common ones, with emphasis on publications dealing with Sulawesi's ichthyofauna (see Kottelat 2013 for nomenclature).

RESULTS

CHONDRICHTHYES

CARCHARHINIFORMES

Carcharhinidae

Requiem sharks: Marine; all oceans (Nelson 2006); enter brackish and freshwaters, including lakes (Grace 2001, Nelson 2006).

***Carcharhinus leucas* (Müller & Henle, 1839)**

Carcharias leucas Müller & Henle, 1839

Potential: Euryhaline; worldwide in subtropical and tropical coastal waters; enter brackish and freshwaters (Compagno 1984, Heupel & Simpfendorfer 2008); no actual records for Sulawesi.

PRISTIFORMES

Pristidae

Sawfishes: Euryhaline; enter brackish and freshwaters; distributed in all tropical and subtropical oceans (Nelson 2006, Wueringer et al. 2009).

Pristis pristis **(Linnaeus, 1758)**
Squalus pristis Linnaeus, 1758
Potential: Euryhaline; worldwide in subtropical and tropical coastal waters; enter brackish and freshwaters; no actual records for Sulawesi (Linnaeus 1758, McEachran & Carvalho 2002).

MYLIOBATIFORMES

Dasyatidae

Stingrays: Marine; distributed throughout the Atlantic and Indo-Pacific; some species enter brackish and freshwaters (Compagno & Roberts 1982, Nelson 2006).

Himantura leoparda **Manjaji-Matsumoto & Last, 2008**
Potential: Euryhaline; enter brackish and freshwaters; no actual records for Sulawesi; distributed throughout the Indo-West-Pacific (Manjaji-Matsumoto & Last 2008).

Himantura uarnak **(Gmelin, 1789)**
Raja uarnak Gmelin, 1789
Potential: Euryhaline; enter brackish and freshwaters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Compagno et al. 1989, Gmelin 1789).

Himantura undulata **(Bleeker, 1852)**
Trygon undulata Bleeker, 1852d
Potential: Euryhaline; enter brackish and freshwaters; no actual records for Sulawesi; distributed throughout the Indo-West Pacific (Last & Stevens 1994).

Himantura tutul **Borsa, Durand, Shen, Alyza, Solihin & Berrebi, 2013**
Potential: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo Pacific; no actual records from Sulawesi (Borsa et al. 2013).

ACTINOPTERYGII

ELOPIFORMES

Megalopidae

Tarpons: Euryhaline; enter brackish and freshwaters; distributed in tropical and subtropical regions (Adams et al. 2013, Nelson 2006).

Megalops cyprinoides **(Broussonet, 1782)**
Clupea cyprinoides Broussonet, 1782
Euryhaline; enter brackish and freshwaters; record from Badjoa, Sulawesi Selatan (Adams et al. 2013, Bleeker 1865a, Coates 1987).

ALBULIFORMES

Albulidae

Bonefishes: Euryhaline; enter brackish and freshwaters; distributed throughout tropical regions (Adams et al. 2013, Nelson 2006).

Albula glossodonta **(Forskål, 1775)**
Argentina glossodonta Forskål, 1775
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Myers 1991, Randall & Bauchot 1999).

ANGUILLIFORMES

Anguillidae

Freshwater eels: Catadromous; adults inhabit freshwaters or estuaries; marine reproduction; juveniles enter freshwaters after metamorphosis; distributed throughout tropical and subtropical regions except the South Atlantic and Eastern Pacific (Arai et al. 1999, Nelson 2006).

Anguilla bicolor **McClelland, 1844**
Catadromous; distributed throughout the Indo-Pacific (Arai et al. 1999, Kottelat 2013); record from Buton (Tweedley et al. 2013).

Anguilla celebesensis **Kaup, 1857**
Anguilla ancestralis Ege, 1939
Catadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Arai et al. 1999); recorded from Lake Tondano, Manado, Sulawesi Utara (Ege 1939), Buton and Kabaena (Tweedley et al. 2013), Lakes of Gorontalo (Haryono & Tjakrawidjaja 2004), Sulawesi Utara (Arai et al. 2003), Sulawesi Tengah (Arai et al. 2003).

Anguilla interioris **Whitley, 1938**
Potential: Catadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific; no actual records for Sulawesi (Arai et al. 1999, Kottelat 2013).

Anguilla marmorata **Quoy & Gaimard, 1824**
Catadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Arai et al. 1999); records from Sulawesi Utara (Haryono et al. 2002), Sulawesi Tenggara (02°56.035'S 121°06.855'E, ZFMK 066057), Sulawesi Selatan (3°41.589'S 119°38.629'E, ZFMK 69560), Lake Poso, Sulawesi Tengah (visual record F.H.).

***Anguilla nebulosa* McClelland, 1844**
Catadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Arai et al. 1999); record from Sulawesi Barat (2°37.368S 119°08.784'E, ZFMK 69701).

***Anguilla obscura* Günther, 1872**
Potential: Catadromus; distributed throughout the Pacific; no actual records for Sulawesi (Arai et al. 1999, Günther 1872a).

Moringuidae
Worm, Spaghetti eels: Euryhaline; enter brackish and freshwaters; fossorial lifestyle; distributed throughout the tropical Western Atlantic and the Indo-Pacific (Nelson 2006, Tsukamoto et al. 2014).

***Moringua guthriana* (McClelland, 1844)**
Ptyobranchus arundinaceus McClelland, 1844
Potential: Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Kottelat 2013); no actual records from Sulawesi.

***Moringua javanica* (Kaup, 1856)**
Aphthalmichthys javanicus Kaup, 1856
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Allen & Steene 1988); record from Buton (Tweedley et al. 2013).

***Moringua microchir* Bleeker, 1853**
Potential: Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Keith et al. 2006); no actual records for Sulawesi.

***Moringua raitaborua* (Hamilton, 1822)**
Moringua latebrosa Schultz, 1953
Euryhaline; enter brackish waters (Kottelat 2013); record from: Kwandang, Gorontalo (Castle 1968, Kottelat 2013, Smith 1994).

Muraenidae
Moray eels: Euryhaline; enter brackish and freshwaters; worldwide distributed in all tropical regions (Nelson 2006, Tsukamoto et al. 2014).

***Gymnothorax polyuranodon* (Bleeker, 1853)**
Muraena polyuranodon Bleeker, 1853f
Potential: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific; no actual records from Sulawesi (Ebner et al. 2011, Tsukamoto et al. 2014).

***Gymnothorax tile* (Hamilton, 1822)**
Muraenophis tile Hamilton, 1822
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Tsukamoto et al. 2014); record from Buton (Tweedley et al. 2013).

***Strophidon sathete* (Hamilton, 1822)**
Muraenophis sathete Hamilton, 1822
Muraena macrurus Bleeker, 1854b
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific; record from Buton (Tweedley et al. 2013).

Ophichthidae
Snake, Worm eels: Marine; some species enter freshwaters; cosmopolitan, distributed throughout tropical regions (Cosker et al. 2012, Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Cirrhimuraena chinensis* Kaup, 1856**
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific; record from Makassar, Sulawesi Selatan (Kaup 1857).

***Lamnostoma mindora* (Jordan & Richardson, 1908)**
Coecula mindora Jordan & Richardson, 1908
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific; record from Buton (Tweedley et al. 2013).

***Muraenichthys gymnopterus* Bleeker, 1852**
Muraena gymnopterus Bleeker, 1852b
Muraenichthys microstomus Bleeker, 1864
Euryhaline; enter brackish waters; distributed throughout the West-Pacific; record from Makassar, Sulawesi Selatan (Bleeker 1864).

***Ophichthus polyophthalmus* Bleeker, 1864**
Potential: Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Kottelat 2013); no actual records from Sulawesi.

***Pisodonophis cancrivorus* (Richardson, 1848)**
Ophisurus cancrivorus Richardson, 1848
Ophisurus brachyosoma Bleeker, 1852b
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific; record from Makassar, Sulawesi Selatan (Bleeker 1852b).

***Yirrkala kaupii* (Bleeker, 1858)**
Sphagebranchus kaupii Bleeker, 1858b
Catadromous; enter brackish and freshwaters; distribute throughout Asia; record from Klabat Diatas, Sulawesi Utara (Bleeker 1858b).

GONORHYNCHIFORMES

Chanidae
Milkfishes: Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Berra 2001; Nelson 2006).

***Chanos chanos* (Forsskål, 1775)**
Mugil chanos Forsskål, 1775
Euryhaline; enter brackish and freshwaters (Allen et al. 2002); record from Sulawesi Selatan (4°07.456'S 119'37.196'E, ZFMK 69759).

CYPRINIFORMES

Cyprinidae
Minnows, Carps: Freshwater; native throughout Africa, Eurasia and North America, introduced worldwide; cyprinids are naturally absent from Sulawesi (Kottelat 1990a, Nelson 2006).

***Barbonymus gonionotus* (Bleeker, 1849)**
Barbus gonionotus Bleeker, 1849a
Introduced: Freshwater; record from Sulawesi Selatan (3°41.589S 119°38.629'E, ZFMK 69514-69516, 69534, 69552-69555), Lake Poso, Sulawesi Tengah (Kottelat 1990b).

***Carassius auratus* (Linnaeus, 1758)**
Introduced: Freshwater; common ornamental fish; breeding form from East Asia; distributed almost worldwide; record from the Malili Lakes system, Sulawesi Selatan (Nasution & Aisyah 2013), Lake Poso, Sulawesi Tengah (Kottelat 1990b).

***Cyprinus carpio* (Linnaeus, 1758)**
Introduced: Freshwater; native to Central Asia; record from Malili Lakes system, Sulawesi Selatan; Lake Poso, Sulawesi Tengah (Kottelat 1990b); aquaculture escapees or stocked specimens (Herder et al. 2012a).

***Cyprinus* cf. *rubrofuscus* (Lacepéde, 1803)**
Cyprinus rubro-fuscus Lacepéde, 1803
Introduced: Freshwater; ornamental carp varieties; possibly derived from *C. fuscus* or hybrids (See Kottelat & Freyhof 2007, and references therein); record from Poso River, Sulawesi Tengah (visual record F.H.).

***Osteochilus vittatus* (Valenciennes, in Cuvier und Valenciennes, 1842)**
Rohita vittata Valenciennes, in Cuvier und Valenciennes, 1842
Osteochilus hasselti (Valenciennes, in Cuvier und Valenciennes, 1842)
Introduced: Freshwater; native to mainland Southeast Asia; records from Malili Lakes system and Lake Sidenreng, Sulawesi Selatan (Omar 2010); Lake Poso, Sulawesi Tengah (visual record F.H.).

CHARACIFORMES

Characidae
Characins: Freshwater; native to Central America, South America, and Africa; without native members in Asia (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Colossoma macropomum* (Cuvier, 1816)**
Myletes macropomus Cuvier, 1816
Introduced: Freshwater; native South America (Santos et al. 2007); record from Lake Matano, Sulawesi Selatan (Herder et al. 2012a) and Lake Poso, Sulawesi Tengah (visual record F.H.).

SILURIFORMES

Plotosidae
Eeltail catfishes: Euryhaline; enter brackish and freshwaters (Nelson 2006, Usman et al. 2013); distributed throughout the Indo-West Pacific (Eschmeyer 2015, Froese & Pauly 2014, Usman et al. 2013).

***Plotosus canius* Hamilton, 1822**
Introduced: Amphidromous; enter brackish and freshwaters (Usman et al. 2013); record from Sulawesi Selatan (04°07.540S 119°37.295'E, ZFMK 066013).

Clariidae
Airbreathing catfishes: Freshwater; native throughout Africa, Syria, South and West Asia (Nelson 2006, Ng & Kottelat 2007); 16 species ocurring in Asia (Ng & Kottelat 2007).

***Clarias batrachus* (Linnaeus, 1758)**
Introduced: Freshwater; native to India, Indochina, Sundaland and the Philippines; neotype from Java, Indonesia (Nelson 2006, Ng & Kottelat 2007); record from the Malili Lake system, Sulawesi Selatan (Herder et al. 2012a); all non-Java specimens are considered as related species-complex (Ng & Kottelat 2007).

CLUPEIFORMES

Engraulididae
Anchovies: Euryhaline; enter brackish and freshwaters; distributed throughout the Atlantic and Indo-Pacific (Nelson 2006, Whitehead et al. 1988).

***Thrissina baelama* (Forskål, 1775)**
Clupea baelama Forskål, 1775
Thryssa baelama (Forskål, 1775)
Potential: Euryhaline; enter brackish waters (Whitehead et al. 1988); no actual records for Sulawesi; distributed throughout the Indo-Pacific (Kottelat 2013).

***Thrissina encrasicholoides* (Bleeker, 1852)**
Engraulis encrasicholoïdes Bleeker, 1851a
Thriyssa *encrasicholoides* Bleeker, 1852a
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Whitehead et al. 1988, Wongratana et al. 1999).

***Thrissina mystax* (Bloch, in Schneider, 1801)**
Stolephorus hamiltoni Bleeker, 1872
Thryssa mystax (Bloch in Schneider, 1801)
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Wongratana et al. 1999); record from Badjoa, Sulawesi Selatan (Bleeker, 1872).

Clupeidae
Herrings, Shads, Sardines: Euryhaline; distributed worldwide (Nelson 2006, Wongratana et al. 1999).

***Herklotsichthys quadrimaculatus* (Rüppell, 1837)**
Clupea quadrimaculata Rüppell, 1837
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Wongratana et al 1999).

MUGILIFORMES

Mugilidae
Mullets: Euryhaline; enter brackish and freshwaters; distributed throughout all tropical and temperate regions (Cuvier & Valenciennes 1836, Durand 2012, Nelson 2006).

***Cestraeus plicatilis* Valenciennes, in Cuvier & Valenciennes, 1836**
Catadromous; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Harrison & Senou 1999); record from Sulawesi freshwaters (Valenciennes, in Cuvier and Valenciennes 1836).

***Mugil cephalus* Linnaeus, 1758**
Catadromous; marine, enter brackish and freshwaters (Harrison & Senou 1997); record from Sulawesi Selatan (4°07.456'S 119'37.196'E, ZFMK 69741, 69760-69763).

ATHERINIFORMES

Telmatherinidae
Sailfin silversides: With exception of *Kalyptatherina helodes*, on islands off the Vogelkop peninsula, restricted to Sulawesi; adaptive radiations in the Malili Lakes: Lakes Matano, Mahalona, Towuti, Lontoa, and connecting / surrounding rivers and streams (Hadiaty & Wirjoatmodjo 2002, Hadiaty et al. 2004, Herder et al. 2006a, b, Pfaender et al. 2011; reviewed by Herder & Schliewen (2010)).

***Telmatherina abendanoni* Weber, 1913**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; predatory, benthic "sharpfin" species of *Telmatherina* (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a).

***Telmatherina antoniae* Kottelat, 1991**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; a "roundfin" *Telmatherina*; the formal name *Telmatherina antoniae* is currently applied to two distinct populations, *T. antoniae* "small" and "large"; males in distinct colour morphs, females with cryptic polymorphism (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a, Herder et al. 2008, Pfaender et al. 2014).

***Telmatherina bonti* Weber & de Beaufort, 1922**
Freshwater; endemic to rivers and streams of the Malili Lakes system, and adjacent systems; enter Lakes Matano, Mahalona and Towuti, Sulawesi Selatan; the only formal name currently available for stream-dwelling *Telmatherina* (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a).

***Telmatherina celebensis* Boulenger, 1897**
Freshwater; endemic to Lakes Mahalona and Towuti, Sulawesi Selatan; additional record from River Tominanga; common in both lakes; males in distinct colour morphs (Hadiaty et al. 2004, Herder et al. 2006a).

***Telmatherina* cf. *celebensis* "Lontoa"**
Freshwater; endemic to Lake Lontoa [also Lantoa or Wawontoa], and surrounding swamps, Sulawesi Selatan; smaller and deeper bodied than *T. celebensis* from Lakes Mahalona and Towuti, Sulawesi Selatan; males in distinct colour morphs (Herder et al. 2006a).

***Telmatherina* "elongated"**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; predatory, benthic "sharpfin" *Telmatherina* with short fins and slender body (Herder et al. 2006a).

***Telmatherina obscura* Kottelat, 1991**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; small, blackish inshore "sharpfin" *Telmatherina* (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a).

***Telmatherina opudi* Kottelat, 1991**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; small "sharpfin" *Telmatherina* predominantly inhabiting well-structured shallows; males in distinct colour morphs (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a).

Telmatherina prognatha **Kottelat, 1991**
Freshwater; endemic to Lake Matano Sulawesi Selatan; large, slender "roundfin" *Telmatherina*; conspicuous "beak-like" jaws; epibenthic, predatory ecology; males in distinct colour morphs (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a).

Telmatherina sarasinorum **Kottelat, 1991**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; benthic "sharpfin" *Telmatherina* specialized on eating eggs of sailfin silversides including conspecifics; males in distinct colour morphs (Hadiaty & Wirjoatmodjo 2002, Cerwenka et al. 2012, Herder et al. 2006a, Gray et al. 2007, Gray et al. 2008a, Gray et al. 2008b, Pfaender et al. 2010).

Telmatherina **"thicklip"**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; benthic "sharpfin" *Telmatherina* specialized on eating shrimps; deep-bodied species, with pronounced "puffy lips" (Herder et al. 2006a, Pfaender et al. 2010).

Telmatherina wahjui **Kottelat, 1991**
Freshwater; endemic to Lake Matano, Sulawesi Selatan; "sharpfin" *Telmatherina* occurring at the outlet of Lake Matano to River Petea, and the shallows of the lake (Hadiaty & Wirjoatmodjo 2002, Herder et al. 2006a).

Paratherina cyanea **Aurich, 1935**
Freshwater; endemic to Lake Towuti and Lake Mahalona, Sulawesi Selatan; slender, conspicuously large-eyed (Hadiaty et al. 2004, Herder et al. 2006a).

Paratherina labiosa **Aurich, 1935**
Freshwater; possibly endemic to Lake Lontoa, Sulawesi Selatan; holotype destroyed (Kottelat 1990c); Kottelat (1990c) tentatively assigned four juveniles obtained in 1989 to *P. labiosa*; further investigations lacking; no records during recent surveys by F.H. in Lake Lontoa.

Paratherina striata **Aurich, 1935**
Freshwater; endemic to Lakes Towuti and Mahalona, Sulawesi Selatan; largest sailfin silverside species; males in distinct colour morphs (Hadiaty et al. 2004, Herder et al. 2006a, Kottelat 1990c).

***Paratherina woltereck*i** **Aurich, 1935**
Freshwater; endemic to Lake Mahalona, Sulawesi Selatan; blackish male colouration (Hadiaty et al. 2004, Herder et al. 2006a).

Tominanga aurea **Kottelat, 1990**
Freshwater: endemic to Lake Mahalona, Sulawesi Selatan; enter rivers; Kottelat (1990c) distinguished *Tominanga aura* from *Tominanga sanguicauda* by male colour traits, gill raker counts, and occurrence (Lake Mahalona vs. Lake Towuti); Herder et al. (2006a) reported less clear indications for species discrimination based on colour traits, and highlight the need for more detailed examinations (Kottelat 1990c, Hadiaty et al. 2004, Herder et al. 2006a).

Tominanga sanguicauda **Kottelat, 1990**
Freshwater; endemic to Lake Towuti, Sulawesi Selatan; enter rivers; see *Tominanga aurea* for notes on species discrimination (Hadiaty et al. 2004, Kottelat 1990c).

Marosatherina ladigesi **(Ahl, 1936)**
Telmatherina ladigesi Ahl, 1936
Freshwater; endemic to the Bantimurung area, Maros karst, Sulawesi Selatan; dwelling in cool karst streams; males with conspicuously elongated blackish rays in second dorsal and anal fins; popular aquarium species (Hadiaty 2007); locally transferred for breeding purposes (F.H., pers. obs.).

Phallostethidae
Priapium fishes: Euryhaline; enter brackish and freshwaters; distributed in Southeast Asia; distinct reproductive morphology: males transfer sperm with a conspicuous priaprium, on the underside of the head (Parenti 1996).

Neostethus djajaorum **Parenti & Louie, 1998**
Euryhaline; endemic to Sulawesi Selatan; brackish waters of coastal plains (Parenti & Louie 1998).

BELONIFORMES

Adrianichthyidae
Ricefishes: Brackish and freshwaters; distributed throughout the West-Pacific; 17 of the 35 species recognized are endemic to Sulawesi, including species flocks in Lake Poso and the Malili Lakes system, endemics in small, remote lakes (*Oryzias hadiatyae*, *O. soerotoi*), one riverine pelvic brooder *O. eversi,* and a riverine lineage species from Southeast Sulawesi (Herder et al. 2012b, Kottelat 1990d, Mokodongan & Yamahira 2015, Parenti 2008, Parenti & Hadiaty 2010, Parenti et al. 2013).

Adrianichthys kruyti **Weber, 1913**
Adrianichthys kruytii (Soeroto & Tungka, 1991)
Freshwater; endemic to Lake Poso, Sulawesi Tengah; pelagic; only a few specimens known (Kottelat 1990b, Parenti 2008).

Adrianichthys oophorus **(Kottelat, 1990)**
Xenopoecilus oophorus Kottelat, 1990a
Freshwater; endemic to Lake Poso, Sulawesi Tengah; pelagic pelvic brooder; abundant in open waters of the lake

in 1995 (Parenti 2008); confirmed by own fieldwork in 2013; caught in the night at the surface; exploited by subsistence fisheries (F.H., pers. obs.).

Adrianichthys poptae **(Weber & de Beaufort, 1922)**
Xenopoecilus poptae Weber & de Beaufort, 1922
Freshwater; endemic to Lake Poso, Sulawesi Tengah; pelagic, rare; not recorded by the authors (Kottelat 1990a, Mokodongan & Yamahira 2015, Parenti 2008, Parenti & Soeroto 2004, Soeroto & Tungka 1991, 1996).

Adrianichthys roseni **Parenti & Soeroto, 2004**
Adrianichthys kruyti (Weber, 1913)
Freshwater; endemic to Lake Poso, Sulawesi Tengah; known from a single collection; likely pelagic; abdominal concavity points towards pelvic brooding (Parenti & Soeroto 2004).

Oryzias asinua **Parenti, Hadiaty, Lumbantobing & Herder, 2013**
Freshwater; endemic to Sulawesi Tenggara; known only from the type locality: Asinua River, regency of Kendari (Parenti et al. 2013).

Oryzias bonneorum **Parenti, 2008**
Xenopoecilus sarasinorum (Rosen, 1964)
Freshwater; endemic to Lake Lindu, Sulawesi Tengah; probably pelagic (Parenti 2008).

Oryzias celebensis **(Weber, 1894)**
Haplochilus celebensis Weber, 1894b
Aplocheilus celebensis Weber & de Beaufort, 1912
Freshwater; records from rivers, streams and Lake Tempe in Sulawesi Selatan (Herder & Chapuis 2010, Parenti 2008), and East Timor (see Parenti 2008).

Oryzias eversi **Herder, Hadiaty & Nolte, 2012**
Freshwater; endemic; reported only from the type locality in Sulawei Selatan, Tana Toraja; Salo Sadang drainage, close to village Tilanga, about 8 km south of Rantepao; the only known riverine Adrianichthyid with pelvic-brooding reproduction (Herder et al. 2012b).

Oryzias hadiatyae **Herder & Chapuis, 2010**
Freshwater; endemic to Lake Masapi, Malili Lakes (Larona) system, Sulawesi Selatan; Lake Masapi is a small and shallow blackwater lake in the hills west of Lake Towuti (Herder & Chapuis, 2010).

Oryzias javanicus **(Bleeker, 1854)**
Aplocheilus javanicus Bleeker, 1854b
Euryhaline; enter brackish waters; distributed from Thailand to Lombok, Borneo and Sulawesi (Parenti 2008); records from Sulawesi Barat (3°20.143S 119°10.179E, ZFMK 69890-69947).

Oryzias marmoratus **(Aurich, 1935)**
Aplocheilus marmoratus Aurich, 1935
Freshwater; endemic to Lakes Towuti, Mahalona, Lontoa [also Lantoa or Wawontoa], and adjacent streams, Sulawesi Selatan; possible hybridization among *O. marmoratus* and *O. profundicola* in Lake Towuti (Herder & Chapuis 2010, Kottelat 1990d, Mokodongan & Yamahira 2015).

Oryzias matanensis **(Aurich, 1935)**
Freshwater; endemic to Lake Matano, Malili Lakes system, Sulawesi Selatan; abundant around the lake; shallows to deeper habitats along the coast (Kottelat 1990d, F.H., pers. obs.).

Oryzias nebulosus **Parenti & Soeroto, 2004**
Freshwater; endemic to Lake Poso, Sulawesi Tengah (Parenti & Soeroto, 2004); small *Oryzias* (up to 33 mm SL); benthopelagic; male courtship at rocky, open deeper habitats (F.H., pers. obs.).

Oryzias nigrimas **Kottelat, 1990**
Freshwater; endemic to Lake Poso, Sulawesi Tengah; benthopelagic, at open habitats in the shallows (Kottelat 1990d, Parenti & Soeroto, 2004); comparatively abundant (F.H., pers. obs.).

Oryzias orthognathus **Kottelat, 1990**
Freshwater; endemic to Lake Poso, Sulawesi Tengah (Parenti 2008); characterized by conspicuously upwards directed mouth, and rounded body (Kottelat 1990d, F.H., pers. obs.); tentatively pelagic, possibly rather benthopelagic (Parenti 2008).

Oryzias profundicula **Kottelat, 1990**
Freshwater; endemic to Lake Towuti, Sulawesi Selatan; lacustrine, deep-bodied *Oryzias* with filamentous fin rays; tends to inhabit deeper inshore habitats (Kottelat 1990d, F.H., pers. obs.).

Oryzias sarasinorum **(Popta, 1905)**
Haplochilus sarasinorum Popta, 1905
Xenopoecilus sarasinorum Regan, 1911
Freshwater; endemic to Lake Lindu, Sulawesi Tengah; slender, pelagic pelvic brooder (Parenti 2008); juveniles recorded in the shallows of the lake in 2013.

Oryzias soerotoi **Mokodongan, Tanaka & Yamahira, 2014**
Freshwater; endemic to Lake Tiu in Sulawesi Tengah, a small (approx. 2 km long) blackwater lake draining to the Laa River; subadults in structured shallows; habitat of adults unknown (Mokodongan et al. 2014).

Oryzias wolasi **Parenti, Hadiaty, Lumbantobing & Herder, 2013**
Freshwater; endemic; small, comparatively deep-bodied *Oryzias* from streams in Sulawesi Tenggara, south of Kendari (Parenti et al. 2013).

Oryzias woworae **Parenti & Hadiaty, 2010**
Freshwater; endemic to Muna island, off Sulawesi Tenggara (Parenti & Hadiaty 2010); small comparatively deep-bodied, with conspicuous, colourful male ornamentation (Parenti & Hadiaty 2010).

Zenarchopteridae
Halfbeaks: Freshwater; distributed in inland and coastal habitats of the Indo-West Pacific; four genera in Sulawesi; *Nomorhamphus* and *Dermogenys* are viviparous, less is known about the reproductive biology of *Tondanichthys* and *Zenarchopterus*; *Nomorhamphus* inhabit hillstreams; 12 species endemic to Sulawesi, especially species-rich (Huylebrouck et al. 2014). Halfbeak taxonomy largely follows the checklist of Collette 2004, supplemented by recent descriptions (Anderson & Collette 1991, Collette 1995, Grier & Collette 1987; Lovejoy et al. 2004, Meisner 2001)

Dermogenys orientalis **(Weber, 1894)**
Hemiramphus orientalis Weber, 1894b
Dermogenys montanus Brembach, 1982
Freshwater: endemic to a hillstream of Maros Karst, Bantimurung, Sulawesi Selatan (Collette 2004, Parenti 2011).

Dermogenys vogti **Brembach, 1982**
Freshwater; most likely endemic to a hillstream on Limestone Mountain at "Topobulu", Sulawesi Selatan [locality not confirmed] (Brembach 1982, Collette 2004, Parenti 2011).

Nomorhamphus brembachi **Vogt, 1978**
Nomorhamphus ravnaki Brembach, 1991
Nomorhamphus ravnaki australe Brembach, 1991
Nomorhamphus sanussii Brembach, 1991
Freshwater; endemic to Maros highland, Sulawesi Selatan (Collette 2004, Parenti 2011).

Nomorhamphus celebensis **Weber & de Beaufort, 1922**
Freshwater; endemic to Lake Poso, Sulawesi Tengah (Collette 2004, Parenti 2011).

Nomorhamphus ebrardtii **(Popta, 1912)**
Hemiramphus (*Dermatogenus*) *ebrardtii* Popta, 1912
Freshwater; endemic to Sulawesi Tenggara; records from Wowoni Island (ZMH 7150); Muna Island, off Sulawesi Tenggara; stream leading to Lake Towuti, Sulawesi Selatan; stream crossing the road Soroako to Malili, 02°38.161'S, 121°12.920'E, ZFMK 49156-49176; Maros Regency, Sungai Abbalu, Village Camba, Camba District, MZB 21295 (Huylebrouck et al. 2014).

Nomorhamphus hageni **(Popta, 1912)**
Hemiramphus hageni Popta, 1912
Freshwater; endemic to Sulawesi Tenggara, Penango and Rumbia valley (Collette 2004, Parenti 2011).

Nomorhamphus kolonodalensis **Meisner & Louie, 2000**
Freshwater; Sulawesi Tengah, Nuha drainage, north of Lake Matano, Sulawesi Selatan, and city of Poso, district of Kolonodale, Sulawesi Tengah (Collette 2004, Meisner & Louie 2000, Parenti 2011).

Nomorhamphus lanceolatus **Huylebrouck, Hadiaty & Herder, 2014**
Freshwater: endemic to Sungai Wawolambo, Sulawesi Tenggara (Huylebrouck et al. 2014).

Nomorhamphus liemi **Vogt, 1978**
Nomorhamphus liemi snijdersi Vogt, 1978
Freshwater; endemic to Maros highland, Sulawesi Selatan (Collette 2004, Parenti 2011, Vogt 1978).

Nomorhamphus megarrhamphus **(Brembach, 1982)**
Dermogenys megarrhamphus Brembach, 1982
Freshwater; endemic to Lakes Towuti and Mahalona, Sulawesi Selatan (Collette 2004; Parenti 2011).

Nomorhamphus rex **Huylebrouck, Hadiaty & Herder, 2012**
Freshwater; disjunct distribution in Sulawesi; records from drainage adjacent to Malili Lakes: Stream Wewu, Cerekang drainage, west of Lake Matano; stream within Malili Lakes drainage: Toletole River at village Toletole; and Sulawesi Selatan, Tana Toraja, about 8 km south of Rantepao (Huylebrouck et al. 2012).

Nomorhamphus sagittarius **Huylebrouck, Hadiaty & Herder, 2014**
Freshwater: Endemic to three streams in Sulawesi Tenggara (Huylebrouck et al. 2014).

Nomorhamphus towoetii **Ladiges, 1972**
Normorhamphus towoetii Ladiges, 1972
Freshwater; records from Lake Towuti, Sulawesi Selatan and Lake Poso, Sulawesi Tengah (Collette 2004, Ladiges 1972, Parenti 2011).

Nomorhamphus weberi **(Boulenger, 1897)**
Hemirhamphus weberi Boulenger, 1897
Freshwater; endemic to Lakes Matano and Mahalona, Sulawesi Selatan (Boulenger 1897, Collette 2004, Parenti 2011).

***Tondanichthys kottelati* Collette, 1995**
Freshwater; endemic to Lake Tondano, Sulawesi Utara; monotypic genus (Collette 1995, 2004, Parenti 2011).

***Zenarchopterus gilli* Smith, 1945**
Freshwater; enter brackish and coastal waters (Donaldson & Myers 2002); record from Sulawesi Selatan (4°07.456'S 119'37.196'E, ZFMK 69726-69740, 69838).

***Zenarchopterus dispar* (Valenciennes, in Cuvier & Valenciennes, 1847)**
Hemiramphus dispar Valenciennes, in Cuvier & Valenciennes, 1847
Zenarchopterus maculosus Garman, 1903
Zenarchopterus vaisiganus Jordan & Seale, 1906
Potential: Freshwater; enter brackish and coastal waters; distributed throughout the Indo-Pacific; no actual records from Sulawesi (Donaldson & Myers 2002, Garman 1903).

CYPRINODONTIFORMES

Aplocheilidae
Rivulines: Freshwater; enter brackish waters; native in the Neotropics, Africa and Southern Asia (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Aplocheilus panchax* (Hamilton, 1822)**
Esox panchax Hamilton, 1822
Possibly introduced: Freshwater; native to India and Southeast Asia; records from Buton (Tweedley et al. 2013), Sulawesi Utara (Haryono et al. 2002), Lakes of Gorontalo (Haryono & Tjakrawidjaja 2004), Sulawesi Selatan (3°41.589'S 119°38.629'E, ZFMK 69557), Sulawesi Barat (2°39.081'S 119°12.436'E, ZFMK 69651), Lake Poso, Sulawesi Tengah (visual record F.H.) and the Malili Lakes system, Sulawesi Selatan (Herder et al. 2012a).

Poeciliidae
Livebearers: Freshwater; enter brackish waters; native to North, Central and South America; several worldwide introduced species (Nelson 2006).

***Gambusia affinis* (Baird & Girard, 1853)**
Heterandria affinis Baird & Girard, 1853
Introduced: Freshwater; native to North and Central America; introduced into warm waters almost worldwide (Pyke 2006); record from Lake Poso, Sulawesi Tengah (visual record F.H.).

***Gambusia holbrooki* Girard, 1859**
Introduced: Freshwater; native to North and Central America; introduced to warm waters almost worldwide; likely confused with G. affinis (Girard 1859, Pyke 2006).

***Poecilia reticulata* Peters, 1859**
Introduced: Freshwater; native to northern South America; introduced almost worldwide; record from Malili Lakes system, Sulawesi Selatan (Herder et al. 2012a), Lake Poso, Sulawesi Tengah (1°46.29'S 120°42.98'E, ZFMK 69801-69803).

GASTEROSTEIFORMES

Syngnathidae
Pipefishes, Seahorses: Catadromous; enter marine, brackish and freshwaters; distributed throughout the Atlantic, Indo-Pacific (Nelson 2006, Wilson & Orr 2011).

***Belonichthys mento* (Bleeker, 1856)**
Syngnathus mento Bleeker, 1856a
Catadromous; record from Manado, Sulawesi Utara (Bleeker 1856a), Buton (Tweedley et al. 2013).

***Coelonotus biocellatus* Günther, 1870**
Potential: Catadromous; no actual records for Sulawesi; distributed throughout the East Indian Archipelago (Günter 1870, cited in Kottelat 2013).

***Coelonotus leiaspis* (Bleeker, 1854)**
Syngnathus leiaspis Bleeker, 1854c
Microphis leiaspis Bleeker, 1854c
Syngnathus budi Bleeker, 1856a
Catadromous; distributed throughout the Indo-Pacific (Dawson 1985); records from Manado, Sulawesi Utara (Bleeker 1856a), Buton (Tweedley et al. 2013).

***Doryichthys boaja* (Bleeker, 1850)**
Syngnathus boaja Bleeker, 1850
Doryichtys spinosus Kaup, 1856
Catadromous; distributed throughout Asia (Dawson 1985); record from Makassar, Sulawesi Selatan (Kaup 1856).

***Hippichthys cyanospilos* (Bleeker, 1854)**
Potential: Catadromous; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Bleeker 1854c).

***Hippichthys heptagonus* Bleeker, 1849**
Potential: Catadromous; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Bleeker 1849b).

***Hippichthys spicifer* (Rüppell, 1838)**
Syngnathus spicifer Rüppell, 1838
Catadromous; distributed throughout the Indo-Pacific (Dawson 1985); record from Sulawesi Selatan (04°14.475'S 119°36.826'E, ZFMK 066326).

Hippocampus waleananus **Gomon & Kuiter, 2009**
Catadromous; endemic to the Togian islands, off Sulawesi Tengah (Gomon & Kuiter 2009).

Lophocampus retzii **(Bleeker, 1856)**
Syngnathus retzii Bleeker, 1856a
Catadromous; distributed throughout the Indo-Pacific; record from Manado, Sulawesi Utara (Bleeker 1856a).

Microphis ocellatus **(Duncker, 1910)**
Doryichthys ocellatus Duncker, 1910
Catadromus; distributed throughout the Indo-Pacific (Dawson 1984); record from Sulawesi Tengah (00°55.395'S 122°52.962'E, ZFMK 066065).

Oostethus brachyurus **(Bleeker, 1854)**
Syngnathus brachyurus Bleeker, 1854c
Syngnathus polyacanthus Bleeker, 1856a
Doryichthys auronitens Kaup, 1856
Catadromous; distributed throughout the Indo-Pacific; record from Manado, Sulawesi Utara (Bleeker 1856a), Makassar, Sulawesi Selatan (Dawson 1985, Kaup 1856).

Oostethus manadensis **(Bleeker, 1856)**
Syngnathus manadensis Bleeker, 1856a
Catadromous; distributed throughout the Indo-Pacific (Dawson 1985); record from Manado, Sulawesi Utara (Bleeker 1856a).

SYNBRANCHIFORMES

Synbranchidae
Swamp eels: Freshwater; entering brackish waters; distributed throughout Central and South America, Mexico, the Indo Australian Archipelago, Asia and West Africa (Nelson 2006, Rosen & Greenwood 1976).

Monopterus albus **(Zuiew, 1793)**
Muraena alba Zuiew, 1793
Introduced: Freshwater; enter brackish waters; records from Sulawesi Utara (Haryono et al. 2002), Malili Lake drainage, Sulawesi Selatan (Herder et al. 2012a).

SCORPAENIFORMES

Tetrarogidae
Wasp fishes: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Eschmeyer 2015, Froese & Pauly 2014 Nelson 2006).

Neovespicula depressifrons **(Richardson, 1848)**
Apistus plagiometopon Bleeker, 1853a
Euryhaline; entering brackish waters; record from Bulukumba, Sulawesi Selatan (Bleeker 1853a).

Tetraroge barbata **(Cuvier, in Cuvier & Valenciennes, 1829)**
Apistus barbatus Cuvier, in Cuvier & Valenciennes, 1829
Euryhaline; enter brackish and freshwaters (Fricke et al. 2011); record from Sulawesi Tengah (00°55.395'S 122°52.962'E, ZFMK 066003).

Tetraroge nigra **(Cuvier, in Cuvier & Valenciennes, 1829)**
Apistus nigra Cuvier, in Cuvier & Valenciennes, 1829
Euryhaline; enter brackish waters; record from Buton (Tweedley et al. 2013).

Platycephalidae
Flatheads: Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Nelson 2006).

Grammoplites scaber **(Linnaeus, 1758)**
Cottus scaber Linnaeus, 1758
Potential: Euryhaline; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Knapp 1999).

PERCIFORMES

PERCOIDEI

Ambassidae
Asiatic glassfishes: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Anderson & Heemstra 2003, Nelson 2006).

Ambassis gymnocephala **(La Cepéde, 1802)**
Lutjan gymnocéphale La Cepéde, 1802
Ambassis dussumieri Cuvier, in Cuvier & Valenciennes, 1828
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Anderson & Heemstra 2003); record from Sulawesi Tengah (00°55.395'S 122°52.962'E, ZFMK 066031-066039).

Ambassis interrupta **Bleeker, 1853**
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Anderson & Heemstra 2003); type locality in Sulawesi (Bleeker 1853c).

Ambassis miops **Günther, 1872**
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Kottelat 2013); record from Buton (Tweedley et al. 2013).

Ambassis urotaenia **Bleeker, 1852**
Potential: Euryhaline; enter brackish and freshwaters (Anderson & Heemstra 2003); no actual records for Sulawesi; distributed throughout the Indo-West Pacific (Bleeker 1852c).

***Ambassis vachellii* Richardson, 1846**
Ambassis telkara Whitley, 1935a
Potential: Euryhaline; enter brackish and freshwaters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Kottelat 2013).

Opistognathidae
Jawfishes: Euryhaline; enter brackish waters; distributed throughout the Western and Central Atlantic and Indo-Pacific (Kottelat 2013; Nelson 2006, Smith-Vaniz 1999).

***Stalix moenensis* (Popta, 1922)**
Gnathypops moenensis Popta, 1922
Euryhaline; enter brackish waters (Smith-Vaniz 1999); record from Muna Island, off Sulawesi Tenggara (Popta1922).

Family Carangidae
Jacks, Pompanos: Marine; juveniles enter brackish waters; distributed throughout the Indo-Pacific and Atlantic (Holland et al. 1996, Nelson 2006).

***Caranx melampygus* Cuvier, in Cuvier & Valenciennes, 1833**
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Holland et al. 1996).

***Caranx papuensis* Alleyne & Macleay, 1877**
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Holland et al. 1996); record from Buton (Tweedley et al. 2013).

***Caranx sexfasciatus* Quoy & Gaimard, 1825**
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Holland et al. 1996).

***Scomberoides lysan* (Forskâl, 1775)**
Scomber lysan Forskâl, 1775
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Smith-Vaniz 1999).

***Selaroides leptolepis* (Cuvier, in Cuvier & Valenciennes, 1833)**
Caranx leptolepis Cuvier, in Cuvier & Valenciennes, 1833
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Smith-Vaniz 1999).

Leiognathidae
Slimys, Slipmouths, Ponyfishes: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Eschmeyer 2015, Froese & Pauly 2014; Nelson 2006).

***Eubleekeria splendens* (Cuvier, 1829)**
Equula splendens Cuvier, 1829
Potential: Euryhaline; no actual records for Sulawesi; distributed throughout the Indo-Pacific; enter brackish waters (Kottelat 2013).

Lutjanidae
Snappers: Euryhaline; enter brackish waters; distributed throughout the Atlantic and Indo-Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Lutjanus argentimaculatus* (Forskål, 1775)**
Sciaena argentimaculata Forskål, 1775
Mesoprion taeniops Valenciennes, in Cuvier & Valenciennes, 1830
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Anderson & Allen 1999); record from Sulawesi freshwaters (Valenciennes, in Cuvier & Valenciennes 1830).

***Lutjanus bohar* (Forskål, 1775)**
Sciaena bohar Forskål, 1775
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-West Pacific (Anderson & Allen 1999).

***Lutjanus ehrenbergii* (Peters, 1869)**
Mesoprion ehrenbergii Peters, 1869
Lutjanus oligolepis Bleeker, 1873a
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Anderson & Allen 1999); record from Makassar, Sulawesi Selatan (Bleeker 1873a).

***Lutjanus fulviflamma* (Forskål, 1775)**
Sciaena fulviflamma Forskål, 1775
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Anderson & Allen 1999).

***Lutjanus fulvus* (Forster, in Schneider, 1801)**
Holocentrus fulvus Forster, in Schneider, 1801
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Anderson & Allen 1999).

***Lutjanus fuscescens* (Valenciennes, in Cuvier & Valenciennes, 1830)**
Mesoprion fuscescens Valenciennes, in Cuvier & Valenciennes, 1830
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Anderson & Allen 1999); record

from Sulawesi freshwaters (Valenciennes, in Cuvier & Valenciennes 1830).

***Lutjanus maxweberi* Popta, 1921**
Lutianus max weberi Popta, 1921
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Anderson & Allen 1999); record from Kali La River, Muna Island, off Sulawesi Tenggara (Popta 1921).

Haemulidae
Grunts: Euryhaline; enter brackish and freshwaters distributed throughout the Atlantic and Indo-Pacific (Eschmeyer 2015, Froese & Pauly 2014).

***Pomadasys argenteus* (Forskål, 1775)**
Sciaena argentea Forskål, 1775
Pristipoma manadense Günther, 1872b
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (McKay 2001); record from Manado, Sulawesi Utara (Günther 1872b).

Nemipteridae
Threadfin breams: Euryhaline; enter brackish waters; distributed throughout the Indo-West-Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Nemipterus peronii* (Valenciennes, in Cuvier & Valenciennes, 1830)**
Dentex peronii Valenciennes, in Cuvier & Valenciennes, 1830
Dentex Smithii Steindachner, 1868
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Russell 2001); record from Tiworo, Muna Island, off Sulawesi Tenggara (Steindachner 1868).

Lethrinidae
Emperors, Scavengers: Euryhaline; enter brackish waters; distributed from West Africa to the Indo-West Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Lethrinus nebulosus* (Forskål, 1775)**
Sciaena nebulosa Forskål, 1775
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Carpenter 2001a).

Polynemidae
Threadfins: Euryhaline; enter brackish and freshwaters; distributed in all tropical and subtropical regions (Motomura 2004, Nelson 2006).

***Polydactylus microstoma* (Bleeker, 1851)**
Polynemus microstoma Bleeker, 1851a
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Feltes 2001); record from Bulukumba, Sulawesi Selatan (Bleeker 1851a).

Sciaenidae
Drums: Euryhaline; enter brackish and freshwaters; Distributed throughout the Atlantic and Indo-Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Nibea soldado* (La Cepède, 1802)**
Holocentrus soldado La Cepède, 1802
Corvina celebica Bleeker, 1854d
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Sasaki 2001); record from Makassar, Sulawesi Selatan (Bleeker 1854d).

Mullidae
Goatfishes: Euryhaline; enter brackish waters; distributed throughout the Atlantic and Indo-Pacific (Eschmeyer 2015, Froese & Pauly 2014; Nelson 2006).

***Upeneus tragula* Richardson, 1846a**
Upeneus sundaicus var. *caudalis* Popta, 1921
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Randall 2001); record from Tiworo, Muna Island, off Sulawesi Tenggara (Popta 1921).

Toxotidae
Archerfishes: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Berra 2001, Nelson 2006).

***Toxotes chatareus* (Hamilton, 1822)**
Coius chatareus Hamilton, 1822
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Allen 1991, 2001).

***Toxotes jaculatrix* (Pallas, in Schlosser, 1767)**
Sciaena jaculatrix Pallas, in Schlosser, 1767
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Allen 1991, 2001).

Terapontidae
Grunters, Tigerperches: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Berra 2001, Nelson 2006, Vari 2001).

***Lagusia micracanthus* (Bleeker, 1860)**
Datnia micracanthus Bleeker, 1860
Therapon (*Datnia*) *micracanthus* Bleeker, 1873b
Terapon micracanthus Fowler, 1931
Papuservus micracanthus Munro, 1958
Euryhaline; endemic to Sulawesi; enter brackish and freshwaters; records from Lagusi, Amparang, Bantimurung,

Cendrana, Leang-leang, Maros, Menralang, Samanggi and Saripa rivers, Manjali Spring, Sulawesi Selatan (Bleeker 1860, Fowler 1931, Vari & Hadiaty 2012).

Terapon jarbua **(Forskål, 1775)**
Sciaena jarbua Forskål, 1775
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Vari 2001); record from Sulawesi Selatan (04°14.475'S 119°36.826'E, ZFMK 066043).

Kuhliidae
Flagtails: Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Berra 2001, Nelson 2006).

Kuhlia marginata **(Cuvier, in Cuvier and Valenciennes, 1829)**
Dules marginatus Cuvier, in Cuvier & Valenciennes, 1829
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Carpenter 2001b); records from Buton (Tweedley et al. 2013), Sulawesi Utara (Haryono et al. 2002), Sulawesi Selatan (3°30.822'S 119°32.267'E, ZFMK 69614-69615).

Kulia rupestris (La Cepède, 1802)
Centropomus rupestris La Cepède, 1802
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Carpenter 2001b); record from Buton (Tweedley et al. 2013).

LABROIDEI

Cichlidae
Cichlids: Diverse group in marine, brackish and freshwater environments; distributed throughout the Neo- and Palaeotropics; not native to Sulawesi; several species introduced worldwide (Berra 2001, Eschmeyer 2015, Froese & Pauly 2014; Nelson 2006).

"Flowerhorn" cichlid
Introduced: Freshwater; hybrid of neotropical species; records from the Malili Lakes system, Sulawesi Selatan (Herder et al. 2012a), Poso River, Sulawesi Tengah (visual record F.H.).

Melanochromis cyaneorhabdos **(Bowers & Stauffer, 1997)**
Introduced: Freshwater; native to Lake Malawi, East Africa; record from the Malili Lakes system, Sulawesi Selatan (Herder et al. 2012) and Lake Poso, Sulawesi Tengah (visual record F.H.).

Oreochromis mossambicus **(Peters, 1852)**
Chromis mossambicus Peters, 1852
Introduced: Freshwater; native to Africa; record from the Malili Lakes system, Sulawesi Selatan (Herder et al. 2012a, Nasution & Aisyah 2013), Lake Poso, Sulawesi Tengah, and various streams (visual record F.H.).

Oreochromis niloticus **(Linnaeus, 1758)**
Introduced: Freshwater; native to Africa; record from the Malili Lakes system (Nasution & Aisyah 2013), Sulawesi Selatan and Sulawesi Barat (2°39.081′S 119°12.436'E, ZFMK 69650).

Scaridae
Parrotfishes: Euryhaline; enter brackish waters; distributed throughout the Atlantic and Indo-Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

Chlorurus sordidus **(Forskål, 1775)**
Scarus sordidus Forskål, 1775
Scarus celebicus Bleeker, 1854d
Euryhaline; enter brackish waters (Bellwood 2001), record from Makassar, Sulawesi Selatan (Bleeker 1854d).

BLENNIOIDEI

Blenniidae
Combooth blennies: Euryhaline; enter brackish and freshwaters; distributed throughout the Atlantic and Indo-Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

Meiacanthus anema **(Bleeker, 1852)**
Petroskirtes anema Bleeker, 1852c
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Allen 1991); record from Kabaena (Tweedley et al. 2013).

CALLIONYMOIDEI

Callionymidae
Dragonets: Euryhaline; two species in freshwaters; distributed throughout the Indo-West Pacific (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

Eleutherochir opercularis **(Valenciennes, in Cuvier & Valenciennes, 1837)**
Callionymus opercularis Valenciennes, in Cuvier & Valenciennes, 1837
Brachycallionymus mirus Herre, 1936
Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Talwar & Jhingran 1991); record from Lembeh Strait, north coast of Sulawesi (Herre, 1936).

GOBIOIDEI

Rhyacichthyidae

Loach gobies: Freshwater; distributed throughout the Indo-West Pacific (Berra 2001, Nelson 2006).

***Rhyacichthys aspro* (Valenciennes, in Cuvier and Valenciennes, 1837)**
Platyptera aspro Valenciennes, in Cuvier & Valenciennes, 1837
Anadromous; enter brackish and freshwaters; distributed throughout Indo-Pacific (Allen 1991); records from Buton (Tweedley et al. 2013), Sulawesi Utara (Haryono et al. 2002), Sulawesi Barat (3°16.651'S 118°51.929'E, ZFMK 6848-6850).

Eleotrididae

Sleepers: Euryhaline; enter brackish and freshwaters; distributed worldwide in tropical and subtropical regions (Berra 2001, Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Belobranchus belobranchus* (Valenciennes, in Cuvier & Valenciennes, 1837)**
Eleotris belobrancha Valenciennes, in Cuvier & Valenciennes, 1837
Anadromous; distributed throughout the Indo-Pacific (Allen 1991); records from Manado, Sulawesi Utara (Valenciennes, in Cuvier & Valenciennes, 1837), Buton and Kabaena (Tweedley et al. 2013), Sulawesi Utara (Haryono et al. 2002) and Sulawesi Barat (2°39.308'S 119°12.095'E, ZFMK 69631; 2°39.081'S 119 12.436'E, ZFMK 69642-69647; 2°38.428'S 119°09.294'E, ZFMK 69670; 2°37.368'S 119°08.784'E, ZFMK 69699).

***Belobranchus segura* Keith, Hadiaty & Lord, 2012**
Freshwater; enter brackish and freshwaters; described from Halmahera and Irian Jaya (Keith et al. 2012); record from Sulawesi Barat (3°16.651'S 118°51.929'E, ZFMK 69814-69815).

***Bostrychus microphthalmus* Hoese & Kottelat, 2005**
Freshwater; endemic to Gua Tanette cave, Sulawesi Selatan; genus poorly defined and likewise poorly known (Hoese & Kottelat 2005).

***Bunaka gyrinoides* (Bleeker, 1853)**
Eleotris gyrinoïdes Bleeker, 1853c
Anadromous; distributed throughout the Indo-West Pacific (Allen 1991); records from Buton (Tweedley et al. 2013), Sulawesi Selatan (3°41.589'S 119°38.629'E, ZFMK 69556, 69558-69559), Sulawesi Barat (3°16.651'S 118°51.929'E, ZFMK 69823).

***Butis amboinensis* (Bleeker, 1854)**
Eleotris amboinensis Bleeker, 1854a
Anadromous; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Yokoo et al. 2006); record from Buton (Tweedley et al. 2013).

***Butis butis* (Hamilton, 1822)**
Cheilodipterus butis Hamilton, 1822
Potential: Anadromous; enter brackish and freshwaters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Allen et al. 2002).

***Eleotris fusca* (Schneider, 1801)**
Poecilia fusca Schneider, 1801
Potential: Anadromous; enter brackish and freshwaters as adults; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Maeda et al. 2007).

***Eleotris melanosoma* Bleeker, 1853**
Anadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Bleeker 1853c, Maeda et al. 2007); records from Sulawesi Selatan (3°30.822´S 119°32.267'E, ZFMK 69595, 69616-69617), Sulawesi Barat (3°16.651´S 118°51.929'E, ZFMK 69806).

***Giuris margaritaceus* (Valenciennes, in Cuvier & Valenciennes, 1837)**
Eleotris margaritacea Valenciennes, in Cuvier & Valenciennes, 1837
Anadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Allen et al. 2002); record from Sulawesi Barat (3°16.651´S 118°51.929'E, ZFMK 69804-69805, 69822).

***Oxyleotris marmorata* (Bleeker, 1852)**
*Eleotris marmorat*a Bleeker, 1852e
Anadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Larson & Murdy 2001); record from Sulawesi Selatan (3°41.589´S 119°38.629'E, ZFMK 69512-69513, 69550-69551).

Gobiidae

Gobies: Euryhaline, catadromous, anadromous and freshwater; includes a total of 1725 species in 251 genera (Berra 2001, Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Acentrogobius janthinopterus* (Bleeker, 1853)**
Gobius janthinopterus Bleeker, 1853b
Gobius hemigymnopomus Bleeker, 1856a
Amphidromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Donaldson & Myers 2002); record from Makassar, Sulawesi Selatan (Bleeker 1853b).

Acentrogobius moloanus **(Herre, 1927)**
Anadromous; enter brackish and freshwaters; distributed throughout the Western Pacific (Blaber & Milton 1990); record from Sulawesi Selatan (119°36.826'E 04°14.475'S, ZFMK 066064).

Amblygobius decussatus **(Bleeker, 1855)**
Gobius decussatus Bleeker, 1855a
Anadromous; enter brackish and freshwaters; distributed throughout the Western Central Pacific (Myers 1991); record from Manado, Sulawesi Utara (Bleeker 1855a).

Awaous grammepomus **(Bleeker, 1849)**
Gobius grammepomus Bleeker, 1849c
Anadromous; enter brackish and freshwaters; distributed throughout Asia (Watson 1992); records from Sulawesi Selatan (3°41.589′S 119°38.629'E, ZFMK 69502-69511, 69535-69549; 3°30.822'S 119°32.267'E, ZFMK 69602-69603, 69628), Sulawesi Barat (2°38.428′S 119°09.294'E, ZFMK 69653-69659; 2°37.915′S 119°09.488'E, ZFMK 69673-69676).

Bathygobius petrophilus **(Bleeker, 1853)**
Gobius petrophilus Bleeker, 1853d
Gobius villosus Weber, 1909
Anadromous; entering brackish and freshwaters; distributed throughout the Indo-West Pacific; record from Manado, Sulawesi Utara (Weber 1909, Weber & de Beaufort 1953).

Cryptocentroides insignis **(Seale, 1910)**
Amblyogobius insignis Seale, 1910
Cryptocentroides dentatus Popta, 1922
Anadromous; entering brackish and freshwaters; distributed throughout the Western Pacific; record from Raha, Muna Island, off Sulawesi Tenggara (Popta 1922).

Drombus bontii **(Bleeker, 1849)**
Gobius bontii Bleeker, 1849c
Acentrogobius elberti Popta, 1921
Anadromous; entering brackish and freshwaters; distributed throughout the Indo-West Pacific (Kottelat 2013); record from Raha, Muna Island, off Sulawesi Tenggara (Popta 1921).

Glossogobius celebius **(Valenciennes, in Cuvier & Valenciennes, 1837)**
Freshwater; endemic to Sulawesi; records from Lake Towuti, Sulawesi Selatan (119°37.295'E 04°07.540'S, ZFMK 066014); Sulawesi Selatan (3°41.589′S 119°38.629'E, ZFMK 69517; 3°30.822'S 119°32.267'E, ZFMK 69596-69601, 69612-69613, 69626-69627), Sulawesi Barat (2°37.368'S 119°08.784'E, ZFMK 69697-69698).

Glossogobius flavipinnis **(Aurich, 1938)**
Freshwater; endemic to Lake Towuti, Sulawesi Selatan; lacustrine dwarf species (Hoese et al. 2015).

Glossogobius intermedius **(Aurich, 1938)**
Freshwater; endemic to Lakes Mahalona and Towuti, Sulawesi Selatan (Kottelat et al. 1993).

Glossogobius matanensis **(Weber, 1913)**
Freshwater; endemic to Lakes Matano, Mahalona, Towuti, and Lontoa, Sulawesi Selatan (Kottelat et al. 1993).

Glossogobius mahalonensis **Hoese, Hadiaty & Herder, 2015**
Freshwater; endemic to Lake Mahalona, Sulawesi Selatan; so far known from one single site within the lake (Hoese et al. 2015).

Gnatholepis anjerensis **(Bleeker, 1851)**
Gobius anjerensis Bleeker, 1851b
Anadromous; enter brackish waters; distributed throughout the Indo-Pacific; record from Bunaken Island, off Manado, Sulawesi Utara (Bleeker, 1851b).

Lentipes mekonggaensis **Keith, Hadiaty, Hubert, Busson & Lord, 2014**
Presumably amphidromous; terra typica is a fast flowing stream in Sulawesi Tenggara (Keith et al. 2014).

Lentipes watsoni **Allen, 1997**
Presumably anadromous; record from Sulawesi Tenggara (02°65.035′S 121°06.855′E, ZFMK 45041); type locality in Papua New Guinea; determination based on one male specimen matching the diagnosis of the species description (Allen 1997).

Lophogobius bleekeri **Popta, 1921**
Anadromous; enter brackish and freshwaters; distributed throughout the Western Pacific; recorded from Raha, Muna Island, off Sulawesi Tenggara (Popta 1921).

Mugilogobius adeia **Larson & Kottelat, 1992**
Freshwater; endemic to Lake Matano, Malili Lakes system, Sulawesi Selatan (Larson 2001, Larson & Kottelat 1992).

Mugilogobius amadi **(Weber, 1913)**
Gobius amadi Weber, 1913
Weberogobius amadi Koumans, 1953
Freshwater; endemic to Lake Poso, Sulawesi Tengah; originally abundant, not reported since 1985 (Larson 2001).

Mugilogobius chulae **(Smith, 1932)**
Vaimosa chulae Smith, 1932
Freshwater; distributed throughout the South-East Asian

archipelago, southern Japan, Sri Lanka, Thailand, Malaysia, Taiwan and Singapore (Huang et al. 2013, Tan & Lim, 2004); record from Boloang, Sulawesi Utara (Larson 2001, Larson et al. 2008).

Mugilogobius hitam **Larson, Geiger, Hadiaty & Herder, 2014**
Freshwater; most likely endemic to Lake Towuti, Sulawesi Selatan (Larson et al. 2014).

Mugilogobius latifrons **(Boulenger, 1897)**
Gobius latifrons Boulenger, 1897
Gobius latifrons Weber, 1913
Vaimosa latifrons Aurich, 1938
Freshwater; endemic to streams and lakes of the Malili Lakes system, Sulawesi Selatan (Larson et al. 2014).

Mugilogobius lepidotus **Larson, 2001**
Freshwater; endemic to Lake Towuti, Malili Lakes system, Sulawesi Selatan; recorded by F.H. in 2002 and 2004.

Mugilogobius mertoni **(Weber, 1911)**
Gobius mertoni Weber, 1911
Tamanka mindora Herre, 1945
Vaimosa layia Herre, 1953
Tamanka mertoni Koumans, 1953
Potential: Anadromous; distributed throughout the Indo-Pacific; no actual records for Sulawesi (Heemstra et al. 2004, Huang et al. 2013, Larson 2001, Larson et al. 2013, Manilo & Bogorodsky 2003).

Mugilogobius rexi **Larson, 2001**
Freshwater; endemic to Lake Mahalona and Lake Towuti, Sulawesi Selatan (Larson 2001).

Mugilogobius sarasinorum **(Boulenger, 1897)**
Gobius sarasinorum Boulenger, 1897
Tamanka sarasinorum Koumans, 1953
Freshwater; endemic to Lake Poso, Sulawesi Tengah; highly abundant in 2013 (F.H. pers. obs.).

Oxyurichthys tentacularis **(Valenciennes, in Cuvier & Valenciennes, 1837)**
Gobius tentacularis Valenciennes, in Cuvier & Valenciennes, 1837
Oxyurichthys rumbia Popta, 1922
Anadromous; enters brackish and freshwaters; distributed throughout the Indo-West Pacific (Maugé 1986); record from Rumbia, Sulawesi Tenggara (Popta 1922).

Periophthalmus kalolo **Lesson, 1831**
Periophthalmus argentilineatus Valenciennes, in Cuvier & Valenciennes, 1837
Anadromous; enter brackish and freshwaters; records from Buton (Tweedley et al. 2013), Sulawesi Selatan (04°14.475′S 119°36.826′E, ZFMK 066001-066002).

Redigobius bikolanus **(Herre, 1927)**
Vaimosa bikolana Herre, 1927
Anadromous; enter brackish and freshwaters; distributed throughout Borneo, Sulawesi and the Philippines (Kottelat et al. 1993); record from Buton (Tweedley et al. 2013).

Redigobius penango **(Popta, 1922)**
Pseudogobius penango Popta, 1922
Anadromous; enter brackish and freshwaters; distributed in Indonesia; record from Penango, Sulawesi Tenggara (Larson 2010, Popta 1922).

Schismatogobius bruynisi **de Beaufort, 1912**
Anadromous; enter brackish and freshwaters; distributed throughout Indonesia and the Philippines (de Beaufort 1912, Keith & Lord 2011, Kottelat & Whitten 1996, Kottelat et al. 1993); record from Sulawesi Tengah (121°06.855’E 02°56.035’S, ZFMK 45049).

Schismatogobius marmoratus **(Peters, 1868)**
Gobiosoma marmorata Peters, 1868
Anadromous; enter brackish and freshwaters; distributed throughout Sulawesi, Philippines and Japan (Keith & Lord 2011, Kottelat et al. 1993); record from Sulawesi Tengah (02°56.035’S 121°06.855’E, ZFMK 066059; 00°55.395’S 122°52.962’E, ZFMK 066060).

Sicyopterus cynocephalus **(Valenciennes, in Cuvier & Valenciennes, 1837)**
Sicydium cynocephalum Valenciennes, in Cuvier & Valenciennes, 1837
Anadromous; enter brackish and freshwaters; distributed throughout Indonesia and the Philippines (Keith & Lord 2011, Koumans 1953); records from Manado harbour, Sulawesi Utara (Valenciennes, in Cuvier & Valenciennes 1837), Sulawesi Utara (Haryono et al. 2002) and Buton (Tweedley et al. 2013).

Sicyopterus longifilis **de Beaufort, 1912**
Anadromous; enter brackish and freshwaters (Allen 1991, Keith & Lord 2011); distributed throughout Seram, Sulawesi, Sumatra and the Philippines (Koumans 1953); records from Sulawesi Utara (Haryono et al. 2002), Sulawesi Selatan (3°27.242’S 119°32.357’E, ZFMK 69563-69573, 69575-69577; 3°30.822’S 119°32.267’E, ZFMK 69604-69609, 69618-69619), Sulawesi Barat (2°39.081’S 119°12.436’E, ZFMK 69632-69641; 2°38.428’S 119 09.294’E, ZFMK 69667-69673; 2°37.915’S 119°09.488’E, ZFMK 69677-69678; 2°37.368’S 119°08.784’E, ZFMK 69689-69696; 3°16.651’S 118°51.929’E, ZFMK 69816-69821, 69837).

***Sicyopterus macrostetholepis* (Bleeker, 1853)**
Sicydium macrostetholepis Bleeker, 1853c
Sicydium gymnauchen Bleeker, 1858a
Anadromous; enter brackish and freshwaters; distributed throughout Indonesia and the Philippines (Allen 1991, 2011, Keith & Lord 2011); record from Manado, Sulawesi Utara (Bleeker 1858a), Buton and Kabaena (Tweedley et al. 2013), Sulawesi Utara (Haryono et al. 2002).

***Sicyopterus microcephalus* (Bleeker, 1855)**
Sicydium microcephalus Bleeker, 1855b
Anadromous; enter brackish and freshwaters; distributed throughout Asia (Allen 1991, Keith & Lord 2011); record from Buton (Tweedley et al. 2013).

***Sicyopterus micrurus* (Bleeker, 1854)**
Sicydium micrurus Bleeker, 1854a
Anadromous; enter brackish and freshwaters; distributed throughout Asia (Allen 1991, Keith & Lord 2011); records from Buton and Kabaena (Tweedley et al. 2013).

***Sicyopus zosterophorus* (Bleeker, 1856)**
Sicydium zosterophorum Bleeker, 1856b
Anadromous; enter brackish and freshwaters; distributed throughout Asia (Allen 1991); record from Sulawesi Barat (3°16.651'S 118°51.929'E, ZFMK 69810-69813, 69835-69836).

***Stenogobius ophthalmoporus* (Bleeker, 1854)**
Gobius ophthalmoporus Bleeker, 1854a
Chonophorus lachrymosus Weber, 1894a
Anadromous; enter brackish and freshwaters; distributed throughout Asia; records from Sulawesi Selatan (Watson 1991, Weber 1894a) and Buton (Tweedley et al. 2013).

***Stiphodon elegans* (Steindachner, 1879)**
Anadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Watson 1995); records from Buton and Kabaena (Tweedley et al. 2013), Sulawesi Tengah (02°56.035'S 121°06.855'E, ZFMK 066027-066028), Sulawesi Selatan (3°27.242'S 119°32.357'E, ZFMK 69578-69584; 3°30.822'S 119°32.267'E, ZFMK 69620-69622), Sulawesi Barat (2°39.081'S 119°12.436'E, ZFMK 69648-69649; 2°38.428´S 119°09.294'E, ZFMK 69667-69669; 2°37.915'S 119°09.488'E, ZFMK 69702-69704; 3°16.651'S 118°51.929'E, ZFMK 69832-69834); specimens recorded outside the Society, Tubuai and Samoa Islands are considered as closely related to *S. elegans* (Kottelat 2013).

***Stiphodon semoni* Weber, 1895**
Anadromous; enter brackish and freshwaters; distributed throughout the Indo-Pacific (Watson 1996); records from Buton (Tweedley et al. 2013), Sulawesi Utara; (Haryono et al. 2002).

***Yongeichthys nebulosus* (Forskål, 1775)**
Gobius nebulosus Forskål, 1775
Acentrogobius nebulosus (Forsskål, 1775)
Potential: Anadromous; enter brackish and freshwaters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Randall et al. 1990).

ACANTHUROIDEI

Scatophagidae
Scats: Euryhaline; enter brackish waters; distributed throughout the Indo-West Pacific (Berra 2001, Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Scatophagus argus* (Linnaeus, 1766)**
Chaetodon argus Linnaeus, 1766
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Allen 1984); record from Buton (Tweedley et al. 2013).

SCOMBROIDEI

Sphyraenidae
Barracudas: Marine; enter brackish waters; distributed in all tropical and subtropical parts of the Atlantic, Indian and Pacific Ocean (Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Sphyraena barracuda* (Edwards, in Catesby, 1771)**
Esox barracuda Edwards, in Catesby, 1771
Euryhaline; juveniles enter brackish waters (Kottelat 2013; Senou 2001); record from Sulawesi Selatan (4°07.456'S 119'37.196'E, ZFMK 69758); original description is a rejected work and not available as a source, author of the species description follows Kottelat (2013).

***Sphyraena obtusata* Cuvier, in Cuvier & Valenciennes, 1829**
Potential: Euryhaline; enter brackish waters; no actual records for Sulawesi; distributed throughout the Indo-Pacific (Senou 2001).

ANABANTOIDEI

Anabantidae
Climbing gouramies: Freshwater; enter brackish waters; distributed throughout the Indo-West Pacific (Berra 2001, Eschmeyer 2015, Froese & Pauly 2014, Nelson 2006).

***Anabas testudineus* (Bloch, 1792)**
Anthias testudineus Bloch, 1792
Anabas variegatus Bleeker, 1851a
Introduced: Freshwater; enter brackish waters; native to India, South and Southeast Asia; record from Kema, Sulawesi Utara (Bleeker 1851a), Malili Lakes system (Na-

Table 1. Summary of species and records according to i) region and ii) salt tolerance / ecology. Total numbers of records and species are highlighted, numbers of introduced and endemic species refer to these total numbers. Species with no actual record for Sulawesi are listed as "potential". Note that obligate and primary freshwater fishes are combined as freshwater fishes. The islands of Buton and Kabaena, off Sulawesi Tenggara, are treated as individual regions (Tweedley et al. 2013).

	Region	Euryhaline	Amphidromous	Anadromous	Catadromous	Freshwater	Total	Introduced	Endemic
Records	Sulawesi Utara	3	-	9	7	5	24	3	1
	Gorontalo	1	-	-	1	1	3	1	-
	Sulawesi Tengah	3	-	3	3	30	39	15	14
	Sulawesi Barat	1	-	7	1	4	13	3	-
	Sulawesi Selatan	23	2	9	5	65	104	19	41
	Sulawesi Tenggara	4	1	6	1	7	19	-	5
	Buton	10	-	13	4	1	28	1	-
	Kabaena	1	-	4	1	-	6	-	-
	Unspecified region	4	-	-	1	1	6	1	3
	Potential	29	-	4	5	1	39	-	-
Species	**Sulawesi**	**77**	**5**	**35**	**20**	**89**	**226**	**22**	**65**

sution & Aisyah 2013), Sulawesi Selatan, Lake Poso, Sulawesi Tengah (Kottelat 1990b, confirmed in 2012 by F.H.).

Osphronemidae
Gouramies: Freshwater; distributed throughout Sumatra, Java and Borneo; able to breath atmospheric air using a specialised respiratory organ (Berra 2001, Kottelat et al. 1993, Nelson 2006).

***Trichopodus* (*Trichogaster*) *pectoralis* Regan, 1910**
Introduced: Freshwater; native to Thailand; record from the Malili Lakes system, Sulawesi Selatan (Herder et al. 2012a, Kottelat et al. 1993,).

***Trichopodus* (*Trichogaster*) *trichopterus* Pallas, 1770**
Introduced: Freshwater; native to Sundaland and Indochina; record from the Malili Lakes system, Sulawesi Selatan (Herder et al. 2012a, Kottelat et al. 1993), Lake Poso, Sulawesi Tengah (Kottelat 1990b, visual record F.H.).

Channidae
Snakeheads: Freshwater; native to tropical Africa and Southern Asia (Berra 2001; Nelson 2006).

***Channa lucius* (Cuvier, in Cuvier and Valenciennes, 1831)**
Ophicephalus lucius Cuvier, in Cuvier and Valenciennes, 1831
Introduced: Freshwater; native to Sundaland and Indochina; record from the Malili Lakes system, Sulawesi Selatan (Kottelat et al. 1993).

***Channa striata* (Bloch, 1793)**
Ophicephalus striatus Bloch, 1793
Introduced: Freshwater; native to India, China and Southeast Asia; records from the Malili Lake system, Sulawesi Selatan (Hadiaty & Wirjoatmodjo 2002, Hadiaty et al. 2004, Herder et al. 2012a), Lake Poso, Sulawesi Tengah (3°41.589'S 119°38.629'E, ZFMK 69518; 3°30.822'S 119°32.267'E, ZFMK 69625) and Sulawesi Barat (2°38.428'S 119°09.294'E, ZFMK 69671-69672).

PLEURONECTIFORMES

Paralichthyidae
Sand flounders: Euryhaline, enter brackish and freshwaters; distributed throughout the Atlantic and Indo-Pacific (Froese & Pauly 2014, Eschmeyer 2015, Nelson 2006).

***Pseudorhombus malayanus* Bleeker, 1865**
Euryhaline; enter brackish waters (Amaoka & Hensley 2001), record from Makassar, Sulawesi Selatan, (Bleeker 1865a).

***Pseudorhombus neglectus* Bleeker, 1865**
Euryhaline; enter brackish waters (Amaoka & Hensley 2001); record from Makassar, Sulawesi Selatan (Bleeker, 1865a).

Soleidae
Soles: Euryhaline; enter brackish and freshwaters; distributed throughout tropical and temperate regions; usually flat, bottom dwelling fishes (Froese & Pauly 2014, Nelson 2006).

***Achirus poropterus* (Bleeker, 1851)**
Euryhaline; enter brackish and freshwaters (Bleeker 1851c); record from Sulawesi Selatan (4°07.456'S 119'37.196'E, ZFMK 69766-69767).

TETRAODONTIFORMES

Triacanthidae
Triplespines: Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Nelson 2006, Santini & Tyler 2002).

***Triacanthus biaculeatus* (Bloch, 1786)**
Balistes biaculeatus Bloch, 1786
Triacanthus russellii Bleeker, 1851d
Euryhaline; enter brackish waters (Matsuura 2001); record from Makassar, Sulawesi Selatan (Bleeker 1851d).

Tetraodontidae
Puffers: Euryhaline; enter brackish and freshwaters; distributed throughout all tropical and subtropical parts of the Atlantic and Indo-Pacific (Nelson 2006, Yamanoue et al. 2011).

***Arothron manilensis* (Marion de Procé, 1822)**
Tetrodon Manilensis Marion de Procé, 1822
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Randall 1985); record from Sulawesi Selatan (04°07.540'S 119°37.295'E, ZFMK 066046-066052).

***Chelonodontops patoca* (Hamilton, 1822)**
Tetrodon patoca Hamilton, 1822
Chelonodon patoca (Hamilton, 1822)
Euryhaline; enter brackish waters; distributed throughout the Indo-Pacific (Talwar & Jhingran 1991); record from Sulawesi Selatan (04°07.540'S 119°37.295'E, ZFMK 060060).

***Dichotomyctere erythrotaenia* (Bleeker, 1853)**
Tetraodon erythrotaenia Bleeker, 1853e
Euryhaline; enter brackish and freshwaters; distributed throughout the Indo-West Pacific (Allen, 1991); record from Maros, Sulawesi Selatan (Bleeker 1853e).

DISCUSSION

Actual records and likely occurrences of fishes in inland waters of Sulawesi sum up to a total of 226 species (see Table 1 for details). This ichthyofauna is composed of 112 genera and 56 families, dominated by Gobiidae (41 species, 18%), Adrianichthyidae (20 species, 9%), Telmatherinidae (19 species, 8%), and Zenarchopteridae (17 species, 7%). Taken together, these four families account for 43% of the island's total inland fish species diversity.

Sulawesi´s native inland ichthyofauna is heterogeneous in terms of salt tolerance: Only 89 species (44% of all native species) are obligate freshwater fishes, whereas 77 species (38% of all native species) are euryhaline. 60 species (29% of all native species) are amphi-, ana- or catadromous, migrating between marine and freshwater environments. 65 species (32% of all native species) of the species inventory are endemic. 46 (71% of all endemic species) of these endemic species are from radiations in the ancient lakes of Sulawesi while only 18 riverine including three euryhaline species are considered endemic. In addition, endemism also appears to be unevenly distributed among the families. Telmatherinidae (19 species), Adrianichthyidae (17 species) and Zenarchopteridae (17 species) contain in sum 86% of all endemic Sulawesi fishes.

In 2011, Parenti reported a total of 76 native freshwater fish species from Sulawesi, of which 56 were considered endemic. This significantly higher number reported here arises to a smaller proportion from additional, recent species descriptions (e.g. Hoese et al. 2015, Huylebrouck et al. 2012, 2014, Larson et al. 2014, Mokodongan et al. 2014, Parenti et al. 2013). However, it is largely due to the wider focus of the present list, which includes all fish species recorded from Sulawesi´s inland waters, also widespread fish species that are very likely to be expected in the island's inland waters, but without actual records.

Sulawesi's freshwater and coastal habitats are facing substantial and manifold threats from habitat degradation (e.g. urbanization, damming, surface mining), and stocking with alien fish species (African cichlids, Asian carps, snakeheads, or gouramis, and others – see Kottelat et al. 1993, Herder, et al. 2012, Tweedley et al. 2013). The list presented here includes 22 introduced species, some of which have been recognized as potential threats to the indigenous fauna of Sulawesi´s ancient lakes (see Herder et al. 2012a for alien fish species recorded in the Malili Lakes area).

The total number of fish species of Sulawesi's freshwater and brackish habitats is significantly lower than that of the Sundaic islands, like closeby Borneo with its at least 430 fish reported species (Kottelat et al. 1993, McGinley & Hogan 2003, Tan 2006; but note that no actual checklist of the inland fishes is available). However, the actual size of Sulawesi is four times smaller than that of Bor-

neo (Rachman et al. 2015). With values between 37% (160 species, McGinley & Hogan 2003) to 62% (267 species, Tan 2006) Borneos rate of endemism is exceptionally high, however the four times smaller island of Sulawesi with its endemism rate of 32% (65 species), appears surprisingly close to its larger neighbour.

The actual state of exploration of the inland ichthyofauna of Sulawesi shows clear regional sampling biases.

However, it appears clear that the total species account of fishes occurring in Sulawesi's inland waters is strongly dominated by the lake species flocks (see also Tweedley et al. 2013, Parenti 2011, Herder & Schliewen 2010), but the exploration of the riverine fish species diversity, and its distribution across the island, remains in a generally fragmentary stage.

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Correction & update

On the Linck collection and specimens of snakes figured by Johann Jakob Scheuchzer (1735) – the oldest fluid-preserved herpetological collection in the world?

Bauer, A.M. & R. Wahlgren (2013). Bonn Zoological Bulletin 62: 220–252

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The contributions of Dr. Konstantin Wöpke to the reorganization of the Linck collection in the Naturalienkabinett Waldenburg have been outlined by Bauer and Wahlgren (2013). Unfortunately, Dr. Wöpke was inadvertently misidentified in Figure 7 (p. 227) of this paper. Originally identified as the figure on the left, he is, in fact, the figure on the right of the photo, wearing a white lab coat. The figure on the left of the photo is the mineralogist Alfred Seifert. This photograph had earlier appeared, correctly labeled, in Budig (1999).

Through the kindness of Mr. Dietrich Wöpke, who has shared some biographical data with me, I am able to provide some further information regarding his father. Konstantin Wöpke was born 29 July 1905 in Crimmitschau, 17 km west of Waldenburg, as the son of Richard and Helene (née Brendel) Wöpke. He attended school in Leipzig until the outbreak of World War I and then continued his schooling in Gotha. He studied zoology, botany, chemistry in Jena, Freiburg im Breisgau and in Leipzig. In 1930 he was promoted to the degree of Dr. phil. on the basis of his dissertation "Die Kloake und die Begattungsorgane der männlichen Zauneidechse (*Lacerta agilis* L.)" completed in Leipzig under the direction of Prof. Dr. Johannes Meisenheimer (1873–1933), a specialist on the development of invertebrates, and published in Jena (Wöpke 1930). He subsequently worked as a teaching assistant at the Zoological Institute of the University of Leipzig and as a research assistant at the Anatomical Institute in Würzburg. From 29 May 1933 to 6 July 1935 he re-organized the approximately 5000 zoological objects in the Fürstlich-Schönburg-Waldenburgische Naturalienkabinett in Waldenburg, struggling with misidentifications, mislabeling, and a century or more of the intermixing of more recently acquired specimens with the 17th and 18th century material of the original Linck collection.

In January 1934 Wöpke passed the state examination for secondary school teachers in the subjects of zoology, botany and chemistry. After graduating from his internship year at the Fürstlich-Schönburgischen Deutschen Oberschule he was employed as a private tutor at the Kammergut in Hardisleben in Thuringia. He was subsequently excluded from school employment by the Saxon Ministry of Education on political grounds and instead, from 1936 to 1939 he served as a research assistant in the Imperial Biological Institute in Naumburg/Saale, where he worked on "Phylloxera in the wine growing areas of Saale and Unstrut." The documentation and results of this work, although apparently unpublished, are maintained in the German Federal Archives. Although he had moved on from Waldenburg, in 1937 Wöpke's opinion was solicited about the renovation of the collections of the Franckesche Stiftungen in Haale (Mojsejenko 2013) and in the same year his guide to the Naturalienkabinett in Waldenburg was published (Wöpke 1937). In August 1939 he was sent to military service and in April 1944 he was killed in Russia. Although Wöpke's scientific career was cut short, his contribution to the reorganization of the Linck collection in Waldenburg is a lasting legacy.

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A new genus and new species of Neotropical Thoracophorini (Coleoptera: Staphylinidae: Osoriinae)

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Abstract. Three new species of the new genus *Geotrochopsis* are described: *G. pubescens*, *G. collaris*, and *G. flaveolus*. The genus is placed in the subtribe Clavilispinina of the tribe Thoracophorini. *G. pubescens* seems to be distributed all over the Neotropical region. Both *G. collaris* and *G. flaveolus* are from Peru and Brazil, respectively. Additionally, one new species is described from the Central Amazon: *Geomitopsis amazonensis*. Furthermore, *Ashnaosorius* Makhan, 2008 is recognised as a new synonym of *Geomitopsis*.

Key words. New species, Osoriinae, Thoracophorini, Neotropics

INTRODUCTION

During the studies on the Neotropical Osoriinae few specimens of blind species were found that belong to the tribe Thoracophorini. Hitherto among this subtribe, only the blind genera *Geomitopsis* Scheerpeltz, 1931 and *Ashnaosorius* Makhan, 2008 were known from the Neotropical region. A more detailed study came to the result that some specimens belong to a new genus. The present paper describes this new genus with its new species. Furthermore, *Ashnaosorius* is a new synonym of *Geomitopsis*. According to Herman (2001) the genus *Geomitopsis* is recorded also from the Mediterranean region from Libanon to Canary Islands with nine species and from Africa with six species. Including the new *Geomitopsis* species, a total of six species is also known from the Neotropics. Therefore, a key to the species of the Neotropical region is provided.

MATERIAL AND METHODS

The material studied in this investigation is presently deposited in the following museums and private collections.

AMNH	American Museum of Natural History, New York
BMNH	British Museum, Natural History, London
INPA	Collections of Instiuto National de Pesquisas da Amazônia, Manaus, Brazil
KNHM	Kansas Natural History Museum, Lawrence
NHMP	National Museum of Natural History, Czec Republic, Prague
ZFMK	Museum Alexander Koenig, Bonn, Germany
JJC	Private collection of Jiří Janák, Prague, Czech Republic
UIC	Private collection of U. Irmler, Plön, Germany

The photographs were taken using a Makroskop M 420 (Wild, Herbrugg) in combination with a digital camera (LeicaEC3). CombineZ5 (Hadley 2006) was used to optimise depth of focus. Length was measured in the middle of tagmata: head from clypeus to posterior edge, pronotum from anterior to posterior edge along midline, elytra from anterior edge of shoulders to posterior edge; width at the widest part of tagmata (head width includes eyes). In the measurement of total length, the abdominal inter-segmental space is subtracted. The aedeagus was dissected and drawings were made using a microscope under 250 x magnification.

DESCRIPTION OF THE NEW SPECIES

Geotrochopsis n. gen.

Type species. *Geotrochopsis pubescens* n.sp. is here designated as the type species

Diagnosis. *Geotrochopsis* is similar to the other blind genus in the tribe Thoracophorini, i.e. *Geomitopsis* Scheerpeltz, 1931. In contrast to *Geomitopsis* Scheerpeltz, 1931, *Geotrochopsis* is densely pubescent on the whole body and the antennomere six is not narrower than antennomeres five and seven. Moreover, the tarsi of *Geotrochopsis* are composed of five tarsomeres, whereas they are

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composed of four tarsomeres in *Geomitopsis*. Additionally, the aedeagus of *Geotrochopsis* is symmetric and without a ventral prominence such as in *Geomitopsis*.

Description. Length and habitus: elongate; blind with reduced elytra; small species of about 1.3–1.6 mm total length.

Head approximately square; clypeus semicircular; labrum divided into two lobes separated by a deep emargination; eyes absent; setiferous punctation; without discrete neck; gular sutures combined.

Antennae not geniculate; width of antennomeres increasing from second antennomere to apex of antenna; penultimate antennomere wider than long.

Pronotum wider than long; sides smoothly rounded; lateral margin fine; with dense setiferous punctation; in posterior half with longitudinal medial impression.

Elytra much wider than long; not longer than pronotum; shoulders widely rounded; divergent from shoulders to posterior angles; hind wings reduced; sutural striae weak or absent; with setiferous punctation.

Abdomen elongate; conically narrowed posteriad; densely pubescent; with microsculpture.

Protibia slightly wider than meso- and metatibia; procoxae slightly elongate; tarsi composed of five tarsomeres.

Aedeagus with broad and stout central lobe; central lobe nearly straight; not or weakly curved; paramera as long as or longer than central lobe: spermatheca oval with short and straight ductus.

Etymology. The specific name is a combination of the Greek words *geo* meaning earth or soil, *trochus* meaning circlet, and *opsis* standing for appearance. The name refers to the similarity to the genus *Allotrochus* Fagel, 1955, and to the soil dwelling life.

***Geotrochopsis pubescens* n. sp.**
Figs 2A, F, 5A, D

Type material. Holotype, male: Peru, Huanuco, Panguana (74°56'W, 9°37'S), rain forest, collected by pitfall trap, April 1984, leg. M. Verhaagh (UIC).

Paratypes: Mexico, 1 female, Veracruz, Córdoba, Paraje Nueve Nacimento, tropical evergreen forest, collected by Berlese method, 7.8.1969, leg. S. & J. Peck (AMNH); Costa Rica, 1 male, 2 females, Vulcan Arenal, rd. to Arenal Observ. Lodge (84°43.58'W, 10°26.51'N), forest border, litter & dead wood, sifted, 3.12.2012, leg. M. Schülke (UIC, MSC); 3 females, Puntarenas, OSA Peninsula, 5km W Rincon de OSA (83°31'W, 8°42'N), 50 m elevation, forest floor, collected by Berlese method, 24.–30.3.1973, leg. J. Wagner & J. Kethley (AMNH); 1 male, Osa Penn., Fundación Neotrop., 10 km W. Rincon (83°31.30'W, 8°42.30'N), 20 m elevation, collected from forest litter by berlese, 23.6.1997, leg. R. Anderson (KNHM); Peru, 1 female, Rio Tambopata Reseve, 30 km SW Puerto Maldonado (69°16'W, 12°12'S), trop. Moist forest, on fungi *Rigidoporus microporus*, 19.9.–10.10.1984, leg. D.A. Grimaldi (AMNH); Brazil, 1 male, São Paulo, leg. Mráz (NMP).

Diagnosis. The species resembles *Geotrochopsis flaveolus* n.sp. (see below) in the structure of the aedeagus and the widely rounded posterior angles of the pronotum. It can be differentiated from *G. flaveolus* by the shorter inner lateral lobes and the longer paramera. The pronotum of *G. flaveolus* is more strongly arched than that of *G. pubescens*, in particular, in the posterior half.

Description. Length: 1.4 mm. Colouration: yellow, legs and antennae light yellow.

Head: 0.19 mm long, 0.29 mm wide; without eyes; temples behind base of antennae approximately as long as clypeus; sides of temples parallel; clypeus semicircular; extremely finely punctate; pubescent; weak netlike microsculpture; surface moderately shiny; small area at base of antennae without punctation and microsculpture; surface shiny.

Antennae as long as head and pronotum combined; first antennomere thick and as long as second and third combined; second antennomere nearly as thick as first, but shorter; third antennomere narrower than preceding and following antennomeres; nearly half as long as second antennomere; following antennomeres increasing in width; penultimate antennomere nearly twice as wide as long.

Pronotum: 0.23 mm long, 0.36 mm wide; widest in middle; evenly narrowed in smooth curve to anterior and posterior margin; anterior angles obtuse; anterior edge not margined; posterior angles widely rounded; posterior edge widely emarginate and distinctly margined; in dorsal aspect, lateral margin fine in anterior half, widened in posterior half and continuous in equal width to wide posterior margin; in central posterior half with finely impressed furrow; punctation deeper and coarser than on head; on average, interstices between punctures as wide as diameter of punctures; pubescent; netlike microsculpture deeper than on head; meshes on average wider than diameter of punctures; surface moderately shiny.

Elytra: 0.22 mm long, 0.38 mm wide; widest at posterior angles; shoulders evenly rounded; with slight obtuse angle, only; sides distinctly margined; posterior edge of elytra straight; punctation slightly finer than on pronotum; irregular microsculpture deeper than on pronotum; pubescent; surface matt; less shiny than on pronotum.

Abdomen as densely and finely punctate as elytra; punctures partly granulate; pubescent; deep netlike microsculpture; surface as matt as surface of elytra.

Aedeagus short and broad; apical lobe shortly curved; paramera distinctly projecting apical lobe; lateral inner lobes transverse and only slightly projecting apical lobe.

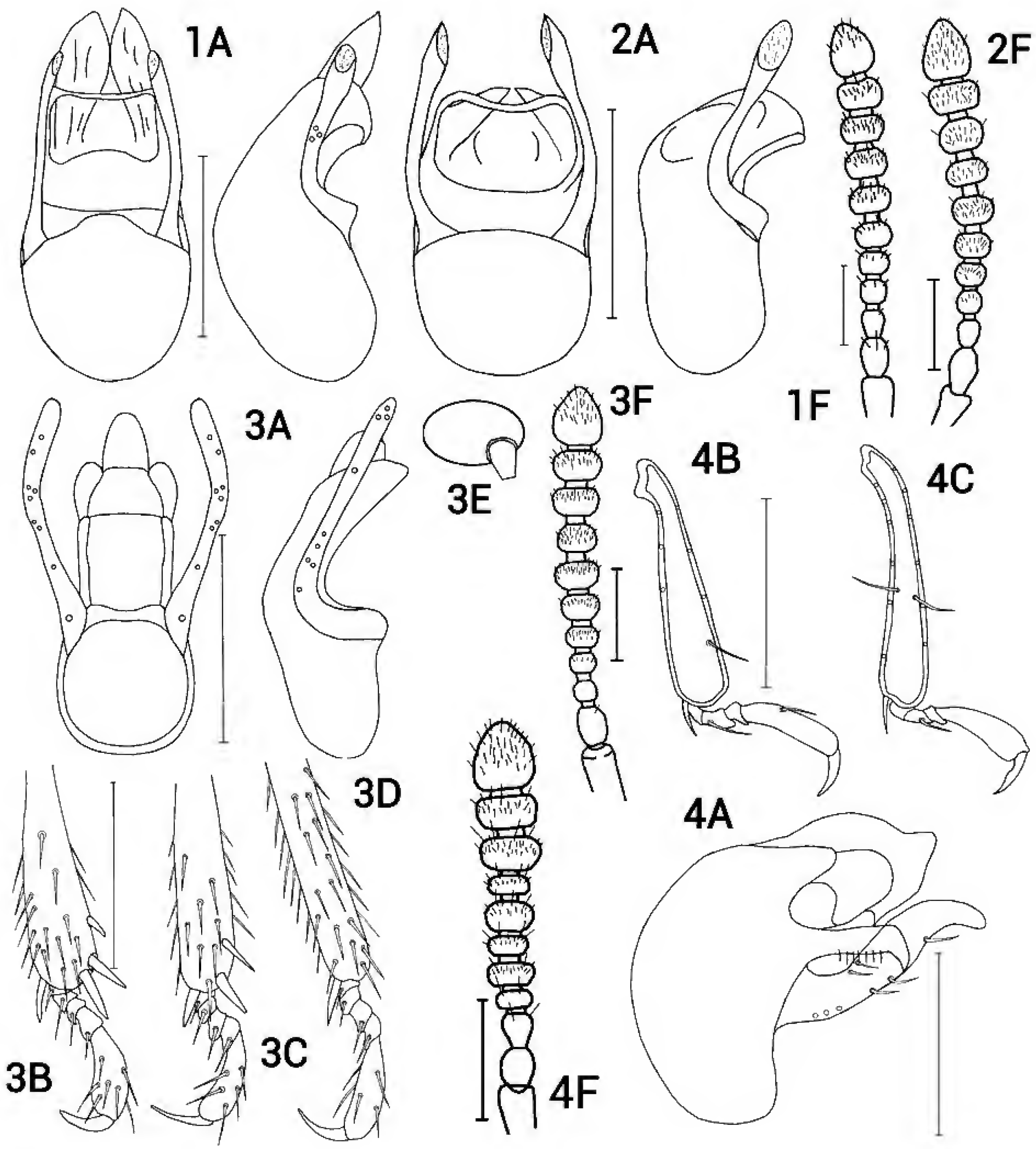

Fig 1–4. *Geotrochopsis flaveolus* (1), *G. pubescens* (2), *G. collaris* (3), and *Geomitopsis amazonensis* (4); Aedeagus in ventral and lateral aspect (A); protibia and tarsi (B); mesotibia and tarsi (C), metatibia and tarsi (D), spermatheca (E), antenna (F); scale bar: 0.1.

Etymology. The specific name pubescens derived from the same Latin name and means pubescent. It refers to the finely hairy punctation.

Geotrochopsis collaris n. sp.
Figs 3A–F, 5C, E

Type material. Holotype, male: Peru, Madre de Dios, Cuzco Amazonica (69°02.06'W, 12°36.48'S), 300 m elevation, secondary forest W1, F95420, 17.5.1995, leg. D. Agosti (AMNH).

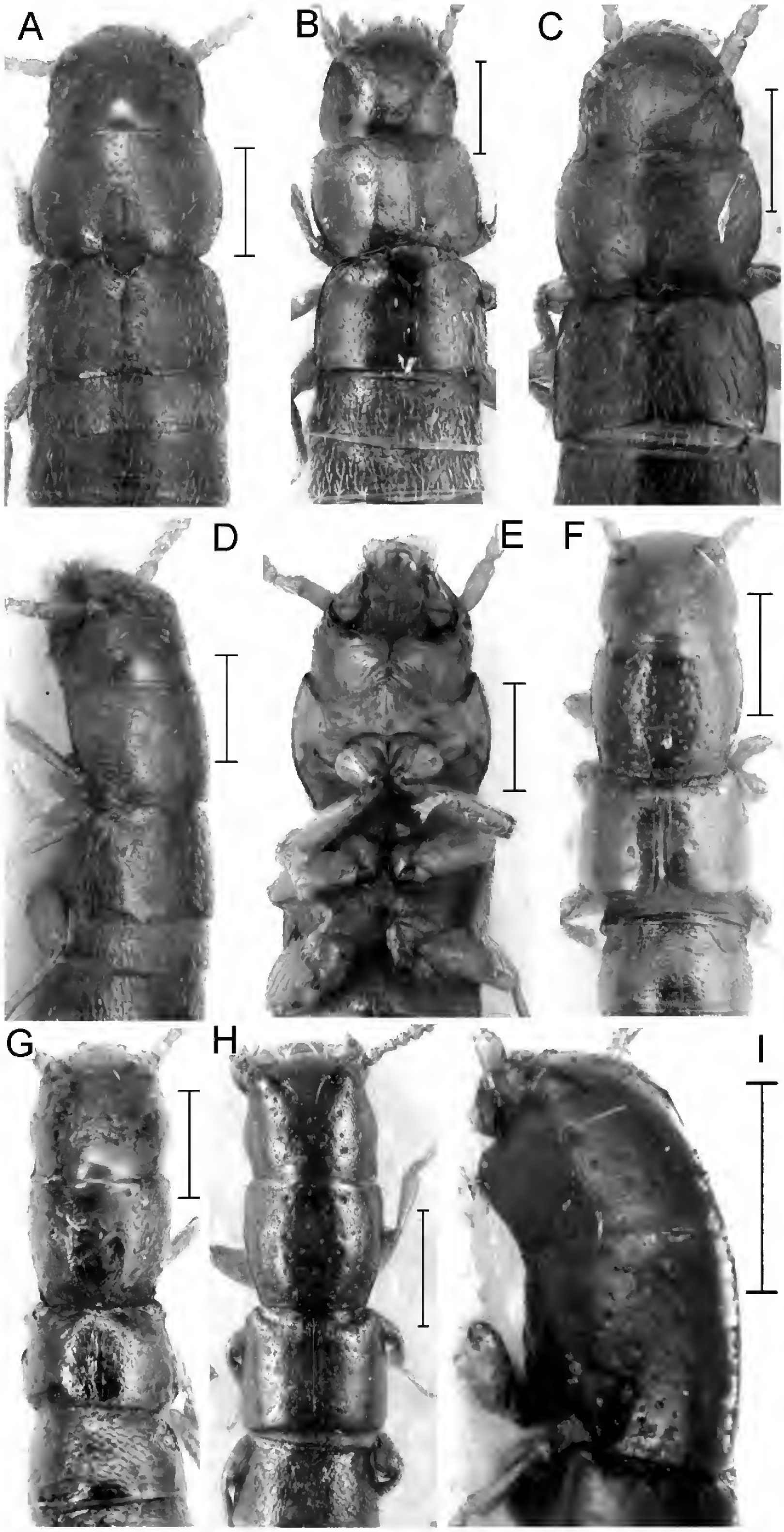

Fig. 5. Dorsal aspect of head, pronotum, and elytra of *Geotrochopsis pubescens* (A), *G. flaveolus* (B), *G. collaris* (C), lateral aspect of *G. pubescens* (D), and ventral aspect of *G. collaris* (E); dorsal aspect of head, pronotum, and elytra of *Geomitopsis amazonensis* (F), and *G. campanae* (G), *G. remilleti* (H), lateral aspect of *Geomitopsis amazonensis* (I); scale bar: 0.2 mm.

Paratypes: 4 males, 16 females with same data as for holotype; 2 females, same location as holotype, but 17.5.1994 (AMNH, UIC).

Diagnosis. The species can be easily differentiated from the other two species by the specific structure of the pronotum. The pronotal sides are slightly emarginate in front of the posterior angles, whereas they are smoothly rounded in the two other species. Furthermore, the posterior edge of the elytra is slightly retreated at suture as triangular emargination and the aedeagus has not the pair of inner lobes as found in *G. pubescens* and *G. flaveolus*.

Description. Length: 1.35 mm. Colouration: dark yellow; antennae and legs lighter yellow.

Head: 0.19 mm long, 0.26 mm wide; without eyes; temples as long as semi-circular clypeus; punctation fine; pubescent; on average, interstices between punctures twice as wide as diameter of punctures; netlike microsculpture moderately deep; meshes distinctly wider than diameter of punctures; surface moderately shiny.

Antennae longer than head and pronotum combined; first antennomere thick and nearly as long as second and third antennomere combined; second antennomere slightly narrower than first, but thicker than third antennomere; twice as long as third antennomere; following antennomeres increasing in width; third antennomere approximately square; penultimate antennomere nearly twice as wide as long.

Pronotum: 0.23 mm long, 0.33 mm wide; widest in middle; evenly narrowed to anterior angles in smooth curve; in front of posterior angles with slight emargination; posterior angles obtuse, but nearly rectangular; anterior edge not margined; lateral margin fine and continuous to posterior edge; margined posterior edge slightly emarginate; punctation slightly denser and deeper than on head; pubescent; on average, interstices between punctures slightly wider than diameter of punctures; netlike microsculpture as deep and wide as on head; surface moderately shiny.

Elytra: 0.21 mm long, 0.35 mm wide; widest at posterior angles; narrowed to shoulders in smooth curve; in dorsal aspect, lateral margin visible in its total length; shoulders obtuse without forming angles; posterior edge of elytra retreated to suture as wide triangular emargination; punctation as deep and dense as on pronotum; microsculpture slightly deeper; surface as shiny as on pronotum.

Abdomen as densely and finely punctate as elytra; punctures partly granulate; pubescent; deep netlike microsculpture; surface as matt as surface of elytra.

Aedeagus slender with long central lobe; apical lobe as long as basal lobe; nearly straight; in slight obtuse angle to basal lobe; slender paramera slightly projecting central lobe; with numerous sensillae; inner lobe projecting.

Etymology. The specific name derived from the Latin word *collum* for pronotum and refers to the specific structure of the posterior angles of the pronotum.

Geotrochopsis flaveolus n. sp.
Figs 1A, F, 5B

Type material. Holotype, male: Brazil, Rio de Janeiro, Moro de Babilónia (43°10'W, 22°57'S), 100–200 m elevation, 25.10.2002, leg. J. Janák (INPA). Paratypes: 172 specimens with same data and from same location as holotype (NHMP, JJC, UIC, ZFMK).

Diagnosis. The species is characterised by the arched pronotum, in particular, in the posterior half. In dorsal aspect, the lateral margin is covered at posterior angles. Furthermore, the pair of inner lobe are longer than in *G. pubescens* and the paramera are shorter.

Description. Length: 1.6 mm. Colouration: Dark yellow; posterior margin of pronotum darker, light brownish; legs and antennae light yellow.

Head: 0.25 mm long, 0.30 mm wide; without eyes; temples as long as semi-circular clypeus; punctation moderately deep and dense; pubescent; on average, interstices between punctures twice as wide as diameter of punctures; netlike microsculpture moderately deep; meshes distinctly wider than diameter of punctures; surface moderately shiny.

Antennae as long as head and pronotum combined; first antennomere long and thick; slightly shorter than second and third antennomeres combined; second antennomere slightly narrower and shorter than first antennomere; conical third antennomere much narrower and shorter than second antennomere; following antennomeres increasing in width; fourth antennomere approximately square; penultimate antennomere nearly twice as wide as long.

Pronotum: 0.25 mm long, 0.39 mm wide; widest in middle; narrowed in even and smooth curve to anterior and posterior angles; posterior angles obtuse; rounded in wide smooth curve without forming distinct angles; anterior edge without margin; lateral margin fine; continuous to posterior edge; in dorsal aspect, margin covered in anterior half and at posterior angles; punctation as dense and deep as on head; pubescent; netlike microsculpture moderately deep; meshes wider than diameter of punctures; with short impressed furrow in posterior half of midline; netlike microsculpture as deep and wide as on head; surface moderately shiny.

Elytra: 0.24 mm long, 0.40 mm wide; widest at posterior angles; slightly narrowed in posterior half; more strongly narrowed in anterior half; shoulders widely rounded; posterior edge of elytra straight; in dorsal aspect, lateral margin visible throughout its total length; contin-

ued to shoulders and ending shortly in front of scutellum; punctation deeper and denser than on pronotum, pubescent; netlike microsculpture slightly deeper than on pronotum, but meshes as wide as on pronotum and wider than diameter of punctures; surface moderately shiny.

Abdomen conically narrowed posteriad; densely punctate and pubescent; punctation still denser than on elytra; punctures partly granulate; netlike microsculpture dense and deep.

Aedeagus broad; apical lobe placed in wide obtuse angle to basal lobe; inner lateral lobes distinctly projecting central lobe; paramera longer than central lobe, but shorter than central lobe and projecting inner lobes combined; group of three sensillae in middle of paramera.

Etymology. The specific name derived from the Latin word '*flaveolus*' meaning yellowish and refers to the overall yellowish colouration of the species.

Key to the species of *Geotrochopsis* n. gen.

1. Posterior angles of pronotum obtusely rounded; aedeagus with pair of inner lobes 2
– Posterior angles of pronotum nearly rectangular, pronotal sides in front of posterior angles slightly sinuate (Fig. 5C), aedeagus with one inner lobe (Fig. 3A) .... *G. collaris* n. sp.
2. Pronotum strongly arched; in dorsal aspect, margin at posterior angles covered (Fig. 5B), pair of inner lobes of aedeagus long, paramera not projecting inner lobes (Fig. 1A) .... *G. flaveolus* n. sp
– Pronotum not arched, in dorsal aspect, margin at posterior angles visible (Fig. 5A), pair of inner lobes of aedeagus short and transverse, paramera projecting inner lobes (Fig. 2A) .... *G. pubescens* n. sp.

Geomitopsis Scheerpeltz, 1931

Ashnaosorius Makhan, 2008: 1, new synonymy.
Libanotyphlus Coiffait, 1954: 155.

Remarks. Makhan (2008) described the new genus *Ashnaosorius* on the basis of two new species from Suriname that were formerly described under the genus *Cubanotyphlus* Coiffait & Decou (1972). He characterised the genus by tarsi being composed of three tarsomeres and differences in the aedeagal structure to *Geomitopsis* Scheerpeltz, 1931. However, he compared his species only with *G. remilleti* Orousset, 1985 that was placed in the subgenus *Pseudogeomitopsis* Orousset, 1983. Fortunately, he published photos of the legs. It can be derived from the photos that the tarsi are not composed of three tarsomeres, as mentioned in the description, but composed of four tarsomeres as in the genus *Geomitopsis*. The first tarsomere is very short and can be easily overlooked. Furthermore, all other characters of *Geomitopsis*, i.e. sixth antennomere narrower than fifth and seventh antennomeres, absence of eyes, the specific structure of the aedeagus, and the overall habitus as derived from the photos of the original publication are equal in *Ashnaosorius* and *Geomitopsis*. Thus, no generic difference between *Ashnaosorius* and *Geomitopsis* is found. Therefore, *Ashnaosorius* is regarded as synonym to *Geomitopsis*.

Unfortunately, the type specimens of the species of *Ashnaosorius* could not be studied. Requests to loan specimens were not answered.

Geomitopsis amazonensis n. sp.

Figs 4A–F, 5F

Type material. Holotype, male: Brazil, Amazonas, Reserva Ducke, 26 km NE Manaus, Plot A, leaf litter, Jan. 1996, leg. M.G.V. Barbosa (BMNH)

Paratypes: Brazil, 2 females from the same location as holotype, but collected on April and Aug. 1995, leg. M.G.V. Barbosa (BMNH); Peru, 1 female, Huanuco, Yuypichis, Panguana (74°56.8'W, 9°37'S), manioca field, 22.9.1975, leg. W. Hanagarth (UIC).

Diagnosis. *G. amazonensis* is characterised by the deep punctation of the pronotum and the elytra. *G. remelleti* Orousset, 1985 has only free larger punctures in a longitudinal row close to the midline. The Chilean species can be distinguished from the Amazonian species by the prominent shoulders.

Description. Length: 1.35 mm. Colouration: light brown, legs and antennae yellow.

Head: 0.17 mm long, 0.22 mm wide; widest shortly in front of posterior margin; clypeus slightly cheek-like extended; without distinctly narrower neck; without eyes; base of antennae to anterior edge; in dorsal aspect; anterior edge even; pair of setiferous punctures between base of antennae and laterally on posterior vertex; punctation weak; only few punctures larger; netlike microsculpture weak; surface shiny.

Antennae slightly longer than head and half of pronotum combined; first antennomere thick; second oval and slightly narrower than first antennomere; third antennomere conical and slightly shorter than second; following antennomeres increasing in width except narrower sixth and eighth antennomeres; antennomere four to ten much wider than long; fourth antennomere twice as wide as long; tenth antennomere slightly wider than twice as wide as long.

Pronotum: 0.23 mm long, 0.25 mm wide; widest near middle; sides evenly narrowed to anterior and posterior angles, but posteriad more strongly narrowed than ante-

riad; posterior angles obtuse; lateral margin continued to posterior edge; anterior edge not margined; punctation much deeper and coarser than on head; narrow midline impunctate; on average, interstices between punctures half as wide as diameter of punctures; in posterior half of midline with oval impression; netlike microsculpture weak, but deeper than on head; surface moderately shiny.

Elytra: 0.21 mm long, 0.28 mm wide; widest near posterior edge; narrowed to shortly rounded shoulders; punctation weaker and sparser than on pronotum; on average, interstices at least as wide as diameter of punctures; two pairs of large circular impressions close to suture; posterior impression larger than anterior impression; three to four setiferous punctures in lateral margin; netlike microsculpture as deep as and as wide as on pronotum; surface moderately shiny.

Abdomen as deeply, but more densely punctate than elytra; netlike microsculpture deeper than on pronotum and elytra; meshes distinctly wider than diameter of punctures; surface less shiny than on pronotum.

Aedeagus with thick central lobe; central lobe with long slender and straight digit ending in acute curved apex; digit at ventral side with row of setae; paramera thick and sinuate; several sensillae on ventral and dorsal side.

Etymology. The specific name derived from the Brazilian state Amazonas, where the species was collected.

Key to the species of *Geomitopsis* in the Neotropical region

1. Pronotum distinctly and densely punctate, elytra with round impressions close to suture (Fig. 5F) .... *G. amazonensis* n. sp.
– Pronotum weakly and sparsely punctate, elytra without impressions 2
2. Shoulders of elytra not carinate, elytra posteriad not dilated (Fig. 5H) 4
– Shoulders of elytra carinate, elytra posteriad dilated (Fig. 5G) 3
3. Pronotum with large impressions on the disc .... *G. campanae* Saiz, 1973
– Pronotum with fine elongate impression in the posterior half of the midline .... *G. chilensis* Coiffait & Saiz, 1963
4. Aedeagus at ventral edge of central lobe with triangular prominence .... *G. amrishi* (Makhan, 2007)
– Aedeagus at ventral edge of central lobe straight, without prominence 5
5. Central lobe of aedeagus at ventral edge straight, with short hook-like apex ..... *G. rishwani* (Makhan, 2007)
– Central lobe of aedeagus at ventral edge evenly curved to acute apex ...... *G. remilleti* Orousset, 1985

DISCUSSION

The new genus *Geotrochopsis* must be certainly placed to the tribe Thoracophorini, as the protibia has no inner emargination with comb such as in the tribe Osoriini. Regarding the united gular sutures, it seems most closely related to the genus *Clavilispinus* Bernhauer, 1926. In contrast to the other blind genus, i.e. *Geomitopsis*, of the same tribe that has four tarsomeres, *Geotrochopsis* has five tarsomeres. Furthermore, *Geomitopsis* was placed to the subtribe Glyptomina by Herman (2001), because gular sutures are separated. Irmler (2010) found that gular sutures can be separated or united even in one genus, which makes their constitution unsuitable for a generic differentiation. Nevertheless, the generic characters, e.g. tarsi composed of five tarsomeres and united gular sutures let suppose that *Geotrochopsis* is closely related to *Clavilispinus*, although the overall habitus is very different. *Clavilispinus* has well developed eyes, a dorsoventrally depressed body, and no pubescence, whereas *Geotrochopsis* is blind with cylindrical body and dense pubescence. It might be also related to *Allotrochus* Fagel, 1955 regarding the overall habitus and the slightly elongate procoxae. But, *Allotrochus* has well developed eyes, no shortened elytra, and no pubescence.

According to Herman (2001) the genus *Geomitopsis* is recorded from Europe, Africa, and South America. Nine species are known from the Mediterranean Europe including northern Africa and Near East, six from tropical Africa, and, together with the newly described species, six species from the Neotropical region. Whereas at present several blind genera are known in the tribe Osoriini, only this genus with blind species was so far known from the tribe Thoracophorini. The genus is characterised by the absence of eyes, tarsi composed of four tarsomeres, shortened elytra, a narrow sixth antennomere, and a characteristic structure of the aedeagus. A similar combination of characters is found in the genus *Arborilispinus* Irmler, 2010. However, *Arborilispinus* has eyes while eyes are absent in *Geomitopsis*.

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A critical review of Hoser's writings on Draconinae, Amphibolurinae, *Laudakia* and Uromastycinae (Squamata: Agamidae)

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Abstract. We analyzed four papers on agamid lizards by self-proclaimed Australian herpetologist Raymond Hoser with respect to the presentation of diagnostic characters as well as their taxonomic and nomenclatural merits. In most cases the taxonomic concepts were lifted from earlier phylogenetic publications and the diagnoses were copied from other authors. Copied text in Hoser's diagnostic section within the analyzed papers amounts to a staggering 83% for Draconinae, 82% for Amphibolurinae, 77% for *Laudakia* and 78% for Uromastycinae, respectively. We found a number of plagiarized paragraphs, sometimes half a page long. Hoser hardly ever makes any effort to attribute statements to the original author and in some cases he even omitted to cite the relevant source. With respect to nomenclature, we found that Hoser proposed names that were preoccupied or unavailable, that a *nomen oblitum* was resurrected incorrectly, *nomina nuda* were produced, a type locality was restricted incorrectly and a questionable holotype was designated for a new species. With respect to taxonomy, we found examples of wrong diagnoses, falsely attributed species, omission of taxa and a lack of understanding or misinterpretation of previously published taxonomic studies on agamid lizards. Furthermore relevant literature on taxonomy and nomenclature has been overlooked or disregarded.

Key words. Plagiarism, IZCN rules, nomina nuda, questionable type specimen designation, ambiguous diagnoses

INTRODUCTION

For the past few years now the *Australasian Journal of Herpetology* (hereafter *AJH*) has been produced in print and as an online journal where pdfs can be downloaded. At the time of writing, 29 issues of the *AJH* have been produced. The editor of and sole contributor to the journal appears to be Raymond Hoser who mainly writes about reptile classification. These articles are an area of controversy and most herpetologists as well as herpetological journals and societies worldwide have recorded their objection to Hoser's works (see Items for Action & Acknowledgments in Kaiser 2013); the scientific community currently appears almost unanimous in their approach not to use Hoser's nomenclature.

Albeit that the majority of herpetologists appears to be in agreement on the suggested suppression of names proposed by Hoser, it has to be noted that this action may not be in agreement with The International Code of Zoological Nomenclature (ICZN, 1999 & 2012; hereafter "the *Code*"), a set of regulation every zoologist is obligated to follow and should wish to uphold. The *Code* is served by the International Commission on Zoological Nomenclature (hereafter, ICZN), which adjudicates instances where taxon names may lead to confusion, are improperly presented or formed, or where published works threaten the stability of the nomenclature in a given discipline. The service of the ICZN includes a recently developed, formal taxon name registration service in the form of Zoobank (accessible at zoobank.org), where authors of taxon names may formally establish a claim to their names or other nomenclatural acts. Hoser registers all names proposed by him with Zoobank and as a consequence the names are available in the sense of the *Code*. However, it must be noted that the Zoobank website does not have any provision to prevent the registration of invalid nomenclatural acts, thus anyone can register and contribute presumed valid scientific names. In its current version,

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Zoobank can only be considered as provisional until there are rules implemented that prevent misuse of this databank.

The *Code* has no provisions for the quality of publication in which taxonomic and nomenclatural acts are proposed. In particular, there is no need for a journal to have an editorial board or have a peer review process in place to validate a proposed name. As has been noted, "the quality of taxonomic descriptions does not make a name unavailable there being no requirement as such in the *Code*…" (Thomson 2014), i.e. for the ICZN nomenclature and taxonomy are not dependent upon each other. A proposed taxonomy may be inconsistent, ambiguous or even false and every herpetologist can choose to follow it or not, but a proposed taxon name, if produced in accordance with the *Code*, becomes available immediately.

There exist only a few prerequisites for a journal to comply with the *Code* in order to validate and make available a proposed name. One such prerequisite (ICZN, Article 8) is that the journal is widely available (for example in public libraries) "providing a public and permanent scientific record" and "numerous identical and durable copies" have to be assured. Typically 25 copies (Recommendation 8b) constitute a sufficiently available edition. In order to prove that sufficient copies have been printed Hoser typically publishes a tax invoice in each issue of *AJH* stating that 50 copies were printed. Distribution is, however, not proven, but presumably at least some copies are sent to libraries (all issues of the journal can be found in the National Library of Australia online catalogue) and distributed among subscribers to the journal. Additionally, all issues or individual articles within a given issue are presented online as downloadable pdfs a month after the print version has been in circulation. Every nomenclatural act is registered with Zoobank and hence the proposed names may be considered published in accordance with the *Code* and therefore available for the purposes of nomenclature.

Editorial boards and high profile referees (reviewers) of manuscripts are usually a measure for the quality of a journal and their names may even be published periodically (e.g. *Journal of Herpetology*). The *AJH* does not have an editorial board to oversee standards of publication or for undisclosed reasons has decided not to present that information in any issues of *AJH*. However, according to Hoser (2012: 41) manuscripts submitted to the journal are refereed by four independent reviewers. This extensive peer review process should assure that all taxonomic and nomenclatural decisions presented "[stand] up to the most robust of scrutiny" (Hoser 2012: 41). Additionally this level of peer review should provide an assurance that the article adheres to commonly accepted editorial standards, including ethical considerations such as avoidance of plagiarism or the inclusion of derogatory comments.

Plagiarism is generally defined as passing off ideas or text from other publications as one's own, whether or not the source is cited (for definitions see plagiarism.org). Copying text into one's own work without citing its source is the most flagrant form of plagiarism and in many countries is a violation of intellectual property rights and illegal. Even copying a substantial part of a previous publication and citing the source is still a form of plagiarism, if the copied text is not produced within quotation marks or other means to make the reader aware that the original research or text is not the work of the current author. Similarly, minor modification of the original text such as rearrangement of phrases or the substitution of a few words is still plagiarism, when the original author is not attributed in an appropriate manner.

Derogatory criticism of other authors in any scientific publication must be avoided. Providing counterarguments relating to scientific opinions of a certain author or a group of authors is a well-established way in science to encourage discussion about the matter in question. However, personal attacks or defamations must be avoided by all means and are not a part of a scientific (or other) publication.

In the following discussion we will analyze four of Hoser's (Hoser 2012a, 2013, 2014b & 2014c) publications on agamid lizards and discuss our findings in taxonomic and nomenclatural terms.

MATERIALS & METHODS

The papers were downloaded from the *AJH* website. Hoser's texts were analyzed with respect to their taxonomic and nomenclatural decisions as well as to generally accepted editorial standards of scientific publications. Previous publications by other authors containing diagnostic characters and descriptions were compared to the diagnoses used by Hoser. Any copied or plagiarized text was marked and attributed to the original source including page number. Hoser's diagnoses do not follow Linnean telegraphic style and frequently contain long introductory sentences that do not further the knowledge about a taxon. We, therefore, accounted for any copied or plagiarized text identified in Hoser's diagnoses in two different ways: 1) as a percentage of the whole diagnosis including introductory sentences and 2) as a percentage of the presented text comprising diagnostic characters only. This was done by accounting for lines of overall text vs. lines of copied text in a way that favoured any originality in Hoser's text, i.e. a line, even if only half printed, was typically counted as full, while in the case of copied text two half lines were counted as one. Total lines in the publication about Amphibolurinae (Hoser 2013) were counted, those of the other publications discussed here were estimated as follows: typically each page in the *AJH* contained about 140 lines (70 lines per column). Abstracts and titles were printed in

full lines and the actual number of lines was therefore doubled as if they had been in two columns. In the case of the other papers the overall sum of lines was not counted but calculated by assuming that each column contains 70 lines.

One of the sources referenced by Hoser (2013) is Cogger (2000). Here we present the results in comparison to Cogger (1983) in order to show that nearly all of the diagnostic characters used for the classification of amphibolurine lizards are considerably older than claimed. Some diagnostic characters could not be accounted for by comparison to earlier publications. Where the source was unclear an internet search was performed and if identified (e.g. Wikipedia, Reptile Database etc.) parts were marked accordingly. Obviously we do not know precisely which sources were actually used by Hoser (original description, review works, catalogues, web pages etc.) and therefore we relate identified text passages to the publication where we looked for and found identical phrases. As we cannot reproduce every single character or paragraph for direct comparison the respective pages where sets of characters or a full description can be found are given together with the number of copied lines and the respective source. At the end of each section we give a summary of our findings with informations on Hoser's taxonomical approach and sources used.

DISCLAIMER

As a general rule Hoser's new taxon names are not used in this paper and the respective taxon named by Hoser will be mentioned as "new tribe / genus to accommodate / contain the following XY" or by a similar phrase where the placeholders are substituted by currently accepted names. This is done to prevent accidental validation of Hoser's names, which subsequently could become available under the rules of the *Code*. If, by accident, a new taxon name proposed by Hoser is used herein that paragraph shall be treated as not published and the name shall be considered as not available for the purposes of nomenclature. This disclaimer is in compliance with Article 8.2 of the *Code*.

RESULTS & DISCUSSION

A) Hoser (2014b) on Draconinae

As printed in the header of the paper, the Draconinae manuscript was received by the journal on 10 November 2013, accepted on 1 June 2014 and published on 1 July 2014. According to the tax invoice, Issue 22 of the *AJH*, which includes the Draconinae paper, appears to have been planned before October 2013, which is the date of the invoice (Hoser 2013: 36, Hoser 2014a: 5; invoice date 3 October 2013, several weeks before the publisher initially received the manuscript). This could indicate that Hoser pays in advance for the printing of issues, which would imply that manuscripts may already be in hand, or that some of the publication dates are otherwise manipulated.

The paper contains the following sections or headings: *Title, Abstract* (including *Keywords*), *Introduction, Unlawful Theft of Material and Data*, and *Notes on Taxa Named Herein*, followed by the actual taxonomic and nomenclatural part, a *Conflict of Interest* section, and a *References Cited* section. The publication additionally contains a table depicting the proposed nomenclature.

The introduction to the paper is mainly concerned with the phylogenetic and morphological data presented by earlier authors, which serve as the basis for Hoser's taxonomic and nomenclatural decisions. As in most of his recent papers, Hoser includes personal criticism of recent and past herpetologists. Similarly, Hoser directly insults several herpetologists in his *Unlawful Theft of Material and Data* section of the paper. In this part we are also made to believe that most of his research files had been confiscated and that his ideas were repeatedly used by recent authors in order to rename taxa and produce junior synonyms.

Overall, in this paper Hoser describes one new species, proposes eight new genera, resurrects three names for subgenera, and erects 22 subgenera, ten new tribes and six subtribes. His diagnosis of the genus *Lyriocephalus* Merrem, 1820 may serve as an example how he defines a genus and how we analyzed his statements. The following is a true copy from Hoser (2014a: 38):

"*Lyriocephalus* Merrem, 1820 is defined by the following suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); tympanum hidden. Five toes. A dorsal crest; a V-shaped gular fold; a bony supraorbital arch. Body compressed, covered with small scales intermixed with enlarged ones. A nuchal and a dorsal crest. A gular sac and a V-shaped gular fold. Adult with a globular hump on the nose. Pre and post-orbital bones forming an arch limiting a supraorbital fossa."

The first set of characters "Mouth large … arch" is a copy from Boulenger's synopsis leading to *Lyriocephalus* (Boulenger, 1885: 251–252). The part in brackets "callous … genera" is taken from a footnote in Boulenger (1885: 251), where it only refers to *Agama* and *Aporoscelis* [= *Xenagama*]. The part containing *Uromastix* [sic] and *Xenagama* could not be identified, but is presumably taken from another comparatively old publication as the genus name *Uromastyx* is written in its historically used form. The second set of characters "Body … fossa" mirrors

Boulenger's (1885: 281) diagnosis of the genus. It is quite obvious that copying has been done without giving it much further consideration. The V-shaped gular fold appears twice as does the dorsal crest. The characters "supraorbital arch" and "supraorbital fossa" are repeated without comment; when a supraorbital arch is formed, this leads to a supraorbital fossa between the arch and the dorsal outer ridge of the eye socket. Hoser cites Moody (1980) in his bibliography. Had he looked at this publication he would have found that as a matter of fact the supraorbital arch in *Lyriocephalus* is formed by prefrontal and postorbital and not as claimed by Hoser (2014a: 38) by "pre and post-orbital bones".

Most taxonomic concepts proposed by Hoser have been published by earlier authors (and cannot be repeated here in full for comparison) but without taking the step of assigning genus names to species groups (e.g., *Gonocephalus* Kaup, 1825; *Draco* Linnaeus, 1758; *Japalura* Gray, 1853) or to species where only insufficient material and/or data exist. In the following we will first provide evidence that the taxonomic scheme proposed by Hoser is either based on previously published concepts or constitutes mere naming of more or less supported nodes in phylogenetic publications concerned with Draconinae. In the second part we will have a closer look at the diagnoses of genera and compare those to previously published material. We will discuss each group in the same sequence as published by Hoser. In our analysis below we will not discuss all of Hoser's diagnoses in such great detail as the one of *Lyriocephalus* and only point out inconsistencies in taxonomy and nomenclature where we feel it should be done for clarity.

The first genus Hoser deals with is *Gonocephalus* which he proposes to divide into five subgenera along with the erection of two new genera. His subgeneric classification follows the species group assignment proposed by Manthey & Denzer (1991) and Denzer & Manthey (2009, part). Denzer & Manthey (l.c.) combined the Philippine species with their *bornensis*/*bellii* species group, which they had considered a separate species group in the earlier publication, based on morphological similarities. Hoser elevates two species to genus rank, namely *G. robinsonii* (Boulenger, 1908) and *G. mjobergi* Smith, 1925. This had already been suggested by Manthey (2010) where *G. robinsonii* was treated as (*Gonocephalus incertae sedis*) *robinsonii* and by Denzer & Manthey (l.c.) where it was suggested that *G. mjobergi* should be referred to as Genus A within a *Gonocephalus* s. l. complex. Owing to insufficient material (only a single female specimen has ever been collected) Denzer & Manthey (l.c.) abstained from proposing a genus name for *G. mjobergi* until more material will become available. They further stated that one autapomorphic character in particular (longitudinal gular folds) constituted a synapomorphy for the genus group *G. mjobergi*, *Mantheyus* Ananjeva & Stuart, 2001 and *Ptyctolaemus* Peters, 1864. With respect to *G. robinsonii* Hoser states in his introductory part to the genus *Gonocephalus* that "no one has bothered to assign the taxon *Gonocephalus robinsonii* … to a genus of its own". As will be discussed below Hoser has taken on this task but fails to deliver as not a single of his characters is of any value to diagnose his newly proposed genus (i.e., differentiate from other genera or species groups).

Initially Hoser characterizes the genus *Gonocephalus*. His diagnosis comprises seven lines and is copied from Boulenger (1885: 282, 3.5 lines) and Denzer & Manthey (2009: 255–256, 3.5 lines). His subgenus to accommodate the *chamaeleontinus* group as defined by Manthey & Denzer (1991) is characterized by a single character copied from Boulenger (1885) and separated from other proposed subgenera by comparison in a way that their full diagnoses are repeated. Hoser considers the *chamaeleontinus* group as the nominate form. Next Hoser proposes a subgenus to accommodate *G. grandis* (Gray, 1845). For this species he resurrects an available name proposed by Gray (1845). The diagnostic character section amounts to approximately 25 lines, all of which are a copy of Boulenger's (1885: 298) description of the species. This is followed by proposing a new subgenus for the Philippine species group by using three characters (two lines) taken from Boulenger (1885). The next new subgenus comprises the *bornensis* group. The diagnostic characters are mainly taken from Boulenger (1885) but rearranged and slightly modified without copying directly. The name he gives the subgenus is different from the name he uses in the keywords to the paper, the latter of which therefore becomes a *nomen nudum*. The last new subgenus proposed contains the Sumatran *megalepis* species group and is characterized initially by two lines copied from Boulenger's (1885) synopsis [key] to the genus followed by Boulenger's (1885: 291) full description of *G. tuberculatus* (= *G. megalepis*). This last part comprises 24 copied lines and ends with citing Boulenger (1885). However, Hoser does not make clear that the whole description is copied by, for example, using quotation marks.

Gonocephalus robinsonii is removed from its synonymy with the genus and a new genus is proposed. This new genus is diagnosed by three characters: karyotype, a "greatly enlarged gular fold" and "a distinctive white lower jaw". The karyotype section is a copy from Diong et al. (2000: 74, 6 lines); the other two characters are supposedly based on Hoser's own research. We would like to note that the karyotype can even vary within a species (e.g., see Ota, 1988 for data on *Japalura swinhonis* Guenther, 1864), the enlarged gular fold is a false character as *G. robinsonii* is the only *Gonocephalus* species without a gular fold, if one considers *G. mjobergi* as not congeneric and the colour of the lower jaw constitutes a variable character in *G. robinsonii* which is dependant on age (see photographs in Manthey 2010).

Gonocephalus mjobergi is accommodated in a new genus. This is done by copying the full description from Denzer & Manthey (2009, 40 lines) including the above-mentioned paragraph about the autapomorphy of longitudinal gular folds. Despite using the complete character set including that a large gular sac "partially conceals the *Gonocephalus*-type typical gular fold" Hoser earlier claims that *G. robinsonii* and *G. mjobergi* have an "enlarged gular fold." Additionally this quote shows that Hoser apparently intended to amend the original statement but ended up doubling an adjective. The original phrase reads: "partially conceals the *Gonocephalus* typical gular fold" (Manthey & Denzer 2009: 257).

Hoser often uses brackets for the author of a taxon and the year of description where he seems to interpret the *Code* in his own way (e.g. he uses brackets for *Gonocephalus robinsonii*, Boulenger, 1908, *G. beyschlagi* Boettger, 1892, *G. doriae* Peters, 1871). The use of brackets for the author/year of a taxon is determined by the ICZN rules (Article 51.3 [Use of parentheses], see ICZN Code for an example). The *Code* prescribes brackets if the allocation of a species changes with respect to a genus. This is not the case here. Boulenger and the other authors decided that the correct spelling should be *Gonyocephalus* (an emendation introduced by Wagler [1830]) albeit that Kaup originally used *Gonocephalus* and later amended it to *Goniocephalus*, but the latter emendation and *Gonyocephalus* are not available under ICZN rules as the original name has to be preserved.

The genus *Japalura* Gray, 1853 is broken up into three genera, two of them divided additionally into two subgenera each. *Japalura* has for a long time been a matter of taxonomic changes and only in recent years are we beginning to understand their phylogenetic relationships. A division into three genera can be derived from molecular phylogenetic analyses, where results indicate that the clades containing *J. variegata* Gray, 1853 / *J. tricarinata* (Blyth, 1853), *J. polygonata* (Hallowell, 1861), and *J. splendida* Barbour & Dunn, 1919 / *J. flaviceps* Barbour & Dunn, 1919 are only very remotely related (e.g., Pyron et al. 2013). Stuart-Fox & Owens (2003) considered *Japalura* as comprised of "two widely divergent goups," named in their analysis as *Japalura* India / *J. variegata*-group and *Japalura* SE Asia / *J. splendida*-group (SE for Southeast). They even mention that they consider both as separate genera. Mahony (2009: 55) refers to the latter species group as "eastern clade". In an earlier publication by Macey et al. (2000) they are referred to as Himalayan and East Asian clades, respectively. Kästle & Schleich (1998) proposed that the species of the Western clade with a visible tympanum should be regarded as a separate genus, for which the name *Oriotiaris* Günther, 1864 was available. Hoser mostly follows these previously published results to propose his taxonomic scheme.

Firstly he deals with *Japalura* species of the nominate genus. Here he seems to accept Mahony's view (2009) that *Japalura* and *Oriotiaris* are congeneric. *Japalura variegata* (type species of *Japalura*) and *J. tricarinata* (type species of *Oriotiaris*) are phylogenetically sufficiently close (Pyron et al., l.c., papers cited in Mahony, l.c.) that Mahony (2009) already suggested to synonymize both genera and treat *Oriotiaris* (resurrected by Kästle & Schleich (1998)) as a junior synonym of *Japalura*. Hoser treats both as subgenera of *Japalura*.

The nominate genus *Japalura* is diagnosed in seven lines which are copied from Boulenger (1885: 307) and Mahony (2010: 4, definition of *Japalura* s.l.) with approximately half of the text from each author. The genus is further divided into a nominate subgenus and by resurrecting an available name for the second subgenus. Hoser first defines *Oriotiaris*. His diagnostic characters for this subgenus are copied from Günther (1864: 150, five lines) and Mahony (2009: 56, five lines). No other characters are given. In the case of one character taken from Mahony (2009) Hoser even copies a typographic error, "…possession of a small gular pouch in the later" [sic!].

The subgenus *Japalura* is diagnosed as follows: "The diagnosis for the nominate subgenus *Japalura* is simply a reversal of the diagnosis for *Oriotiaris*." Hoser distinguishes *Japalura* from his subgenus *Oriotiaris* as follows: "*Oriotiaris* is further separated from the nominate subgenus *Japalura* by the absence (vs. presence) of dorsal chevrons and presence (vs. absence) of a coloured gular region, concealed tympanum, large crest spines in males and erectile nuchal crest (roach), in members of *Japalura*." *Japalura tricarinata* is highly variable and capable of changing colour. There exist photographs of completely green individuals without any chevron pattern (see for example Manthey 2010: 98, Fig RA02806-4). On the other hand, *J. planidorsata* Jerdon, 1870 does not have an erectile nuchal crest nor does *J. sagittifera* Smith, 1940 both of which are placed by Hoser in the nominate subgenus.

For *Japalura polygonata* Hoser resurrects its original name *Diploderma polygonatum* Hallowell, 1861. Phylogenetic studies showed that *J. polygonata* is only remotely related to other *Japalura* but seems to be the sister taxon of *Gonocephalus robinsonii* (Pyron et al. 2013). *Diploderma polygonatum* was already suggested by Mahony (2009: 55) in case the eastern clade (see below) should turn out to be monophyletic. The genus is diagnosed with four lines, all of which are copied from Boulenger (1885: 307).

Having already dealt with the *variegata* group, Hoser proceeds to define a new genus for the eastern species group, which he splits into two subgenera. The new genus to accommodate all East Asian *Japalura* species is defined in the space of approximately nine lines, seven of which are directly copied from Boulenger (1885: 307–308). One

character is the negation of a Boulenger character and the rest are slightly amended but not identically copied from Mahony (2009). No new characters are introduced by Hoser. This genus is split into two subgenera on the basis of Boulenger's synopsis (1885:308) the differences being the length of the tibia and presence or absence of a longitudinal fold. For *J. swinhonis,* Hoser claims that the "tibia is as long as the skull". Already Stejneger (1907: 183) pointed out that in two old males he had studied "the tibia is decidedly shorter than the skull". With respect to the second character we would like to note that *J. chapaensis* Bourret, 1937, *J. fasciata* Mertens, 1926, *J. grahami* (Stejneger, 1924) and *J. micangshanensis* Song, 1987 do not have a longitudinal fold as claimed by Hoser. They would therefore have to be transferred to his first subgenus.

The genus *Calotes* Daudin, 1802 is divided into three genera, of which two are further divided into subgenera (the nominate genus into five and a newly proposed genus into four subgenera). The basis for this taxonomic scheme appears to be the result of the extensive molecular biological studies presented by Zug et al. (2006) and Pyron et al. (2013). The proposed scheme clearly reflects the nodes in previously published phylogenetic trees. A division into three groups was already proposed by Smith (1935) who differentiated between a *C. versicolor* group, a *C. liocephalus* group and a group comprising *C. rouxi* Duméril & Bibron, 1837 and *C. ellioti* Günther, 1864. The first and last of Smith's groups are elevated to genus level by Hoser, the *liocephalus* group is considered by Hoser as a subgenus.

Initially the genus *Calotes* is diagnosed by a copy of Boulenger's diagnosis (1885:314, four lines) and subsequently compared to his newly erected genera (see below). The first subgenus described within *Calotes* serves to accommodate *C. calotes* (Linnaeus, 1758) and *C. htunwini* Zug & Vindum, 2006. Their close relationship was discovered in phylogenetic studies despite the fact that their distribution is rather disjunct. The nominate subgenus is defined by Hoser by initially repeating Boulenger's key (1885: 315–316, 3.5 lines) leading to *C. ophiomachus* (= *C. calotes*) and subsequently by a complete copy of Boulenger's description of the species (Boulenger 1885:327, approximately 18 lines). By stating that all of these characters define the subgenus Hoser renders his diagnosis false. *C. htunwini* does not have a nuchal crest where the height "equals or exceeds the diameter of the orbit" nor does it have a "dorso-nuchal crest composed of closely set lanceolate spines" nor is this species green above. Additionally we like to note that already Boulenger's description contains a mistake in stating that in *C. calotes* a "gular sac is not developed". This has been copied by Hoser; however, male *C. calotes* actually have a reasonably well developed gular sac during the breeding season as have *C. htunwini* but to a lesser extent.

Next Hoser proposes a new subgenus containing species allied to *Calotes versicolor* (Daudin, 1802) by copying 1.5 lines from Boulenger's synopsis (Boulenger 1885: 314–315) followed by an entirely copied description of *C. versicolor* from Boulenger (1885: 312, 20 lines). Here also Hoser repeats Boulenger's statement that in *C. versicolor* the "gular pouch [is] not developed" which is not true for male specimens during the breeding season (Smith 1935; numerous photographs on the internet). Hoser does not present any new characters for the *C. versicolor* group. Subsequently Hoser erects a new subgenus containing two closely related species from the Western Ghats, namely *C. nemoricola* Jerdon, 1853 and *C. grandisquamis* Günther, 1875. To diagnose the genus he initially copies four lines from Boulenger's synopsis (1885: 315) leading to these species followed by the reproduction of Boulenger's description (1885: 326) of *C. nemoricola* (approximately 20 lines). No additional or new characters are presented by Hoser.

Species allied to *Calotes liolepis* Boulenger, 1885 (*C. nigrilabris* Peters, 1860 and *C. desilvai* Bahir & Maduwage, 2005) are the content of a subgenus that is initially defined by repeating in full Hallermann's key (2000: 161–162) leading to *C. nigrilabris* and *C. liolepis*, respectively (3.5 lines each), followed by a copy of Boulenger's descriptions (1885: 327–328) of *C. nigrilabris* (approximately 22 lines) and *C. liolepis* (approximately 15 lines). No other characters are presented in the diagnosis.

Species related to *Calotes liocephalus* Günther, 1872 are placed by Hoser into a new subgenus which again is defined by the characters given in Hallermann's key (2000) here for *C. liocephalus* and *C. ceylonensis* Müller, 1887 (3.5 lines each) followed by the respective descriptions copied from Boulenger (1885: 329) for *C. liocephalus* (18 lines) and Boulenger (1890: 139–140) for *C. ceylonensis* (13 lines) without presenting any further characters.

The last subgenus within *Calotes* proposed by Hoser is monotypic and contains only *C. aurantolabium* Krishnan, 2008. Diagnostic characters are given in the space of 13 lines all of which are a copy of Krishnan (2008).

After having dealt with the species he considers *Calotes* sensu stricto. Hoser proceeds to erect a new genus to accommodate species related to *C. mystaceus* Duméril & Bibron, 1837. This genus is further divided into four subgenera. The definition of the genus comprises approximately 13 lines, which are a copy from Boulenger (1885: 315) or may partially have been taken from Hallermann (2000: 162). Initially Hoser gives a short diagnosis for the genus (2.5 lines) followed by the sentence: "In addition to this, each of the relevant subgenera are further diagnosed and separated from the other genera by one or other of: A/ [diagnosis subgenus A] or B/ [diagnosis subgenus B] or C/ [diagnosis subgenus C]". This is followed by separating the genus from *Calotes* and another genus containing *C. rouxii* Duméril & Bibron, 1837 and *C. ellioti* Gün-

ther, 1864. The presentation of his diagnoses for the subgenera here is peculiar if not unique: the diagnostic characters including comparisons presented for the nominate subgenus and two other subgenera are absolutely identical to that of the genus!

The last subgenus is monotypic and erected for *Calotes nigriplicatus* Hallermann, 2000. Here he repeats the full description as given by Hallermann (2000: 156, 158, approximately 30 lines) only adapted in places where a comparison is made to one of his newly erected subgenera (i.e. the name *Calotes* is replaced by Hoser's new name). This is followed by repeating again his diagnostic characters for the already defined subgenera and genera. In the space of two pages he uses the same 22 lines five times. In all of this Hoser does not present a single new character.

Next he defines a new genus to accommodate *Calotes rouxii* and *C. elliot*i. The diagnosis comprises two lines and is copied from Hallermann's key (2000: 162).

The last genus Hoser proposes is again monotypic and only contains what he calls *Calotes andamanensis*, currently considered as *Pseudocalotes andamanensis* (Boulenger, 1891). While Harikrishnan & Vasudevan (2013: 11) state: "…these differences are not sufficiently pronounced to justify the recognition of a new genus. In the absence of a molecular phylogeny and based on external morphology alone, it is most appropriate to consider this species as a member of *Pseudocalotes*…" Hoser opposes this by writing "is also sufficiently divergent to warrant being placed in a separate genus". Hoser's initial diagnosis is a complete copy (31 lines) from Krishnan's description (2008: 533) of the species, only substituted with Hoser's nomenclature in places where Krishnan made comparisons with *Calotes*. This is followed by the description of *Pseudocalotes andamanensis* (14 lines) given by Harikrishnan & Vasudevan (2013: 11) and subsequently by yet another short description of this species including comparisons with *Calotes* Daudin, 1802, *Bronchocela* Kaup, 1827, *Complicitus* Manthey in Manthey and Grossmann, 1997, *Salea* Gray, 1845, and *Dendragama* Doria, 1888 (17 lines) as produced on the Reptile Database website (original publication not identified). We note that also the first two descriptions are available on the Reptile Database website. Hence Hoser could have copied the whole diagnosis from there without even consulting the original publications. This assumption is viable as Harikrishnan & Vasudevan (l.c.) are cited in an identical place to that on the website and Krishan's description stays without a citation as this is also the case on the website. Altogether he "describes" the species three times in 65 lines of which 62 lines are copied from other sources and the remaining lines are introductory sentences.

The genus *Ceratophora* Gray, 1835 is divided into three genera including two subgenera reflecting the molecular and morphological (rostral horn appendage) phylogeny of Schulte et al. (2002). The nominate genus contains the species related to *C. stoddartii* Gray, 1834 which is divided subsequently into two subgenera. Hoser's description of the nominate genus is presented in 6.5 lines all of which are taken from Boulenger (1885: 277) with only minor changes. This is followed by a separation from his other proposed subgenus and the other two proposed genera (12 lines). The complete text to describe the diagnostic character is copied from Boulenger (1885: 277) and Pethiyagoda & Manamendra-Arachchi (1998: 1, 4). The definition of his subgenus to accommodate *C. tennentii* Günther, 1861 comprises approximately four lines all of which are taken from Boulenger's synopsis (1885: 277). The nominate subgenus is defined by four lines again from Boulenger (1885: 277).

Next Hoser erects a new genus for *Ceratophora aspera* Günther, 1864, which is initially defined by two lines from Boulenger (1885: 277) followed by characters taken from Pethiyagoda & Manamendra-Arachchi (1998: 44, 46, six lines, all copied) to separate it from the other proposed genera by Hoser. Even the distributional data are copied verbatim from Pethiyagoda & Manamendra-Arachchi (1998: 44).

The last genus Hoser proposes for this group of lizards only contains *Ceratophora karu* Pethiyagoda & Manamendra-Arachchi, 1998. This is presented including comparisons within approximately eight lines, all of which are a copy from Pethiyagoda & Manamendra-Arachchi (1998: 44) and can partially be found in an identical way on the Reptile Database website.

Next Hoser deals with the lizards of the genus *Bronchocela* Kaup, 1827. He initially gives an introduction where he seems to restrict the type locality of *B. cristatella* (Kuhl, 1820) and to resurrect *B. moluccana* (Lesson, 1830) (see discussion below). The genus is divided into two subgenera the first of which contains *B. jubata* (Duméril & Bibron, 1837) and *B. orlovi* Hallermann, 2004. The first three lines of the diagnosis are taken from Boulenger (1885: 314 all copied) and a full description (approximately 20 lines) of *B. jubata* is presented by a copy of Hallermann's description (2005: 171–172). Two more lines of characters concerning the scales at the base of the dorsal crest could have been taken from de Rooij (1915: 123). One character cannot be retraced to earlier publications and presumably comes from Hoser's research: "The dorsal crest gives the appearance as if it is composed of tiny hairs as opposed to scales (as seen in *Bronchocela*)" [sensu Hoser]. We note that adult males of *B. jubata* have one of the most developed dorsal crests among *Bronchocela,* consisting of lanceolate scales.

The only new species described by Hoser within the Draconinae paper is a member of *Bronchocela* Kaup, 1827 and refers to material collected on Halmahera Island, Maluku Province, Indonesia. His description of this species is purely based on colouration and an elongated scale between the nasal and the rostral. We note that most

– if not all – *Bronchocela* species are capable of extreme colour changes. A typically brightly green coloured *B. cristatella* (Kuhl, 1820) may become completely black when disturbed or during copulation (WD pers. obs.). Hoser's choice of holotype (USNM 237431) is – to put it mildly – slightly confusing. The specimen he chose actually has a bifurcated tail something that should have been noted in the diagnosis (see collections.si.edu/search/results.htm?q=record_ID:nmnhvz_6091296). We further note that the gender of *Bronchocela* is female but Hoser creates a species name with a masculine ending. The description of his new *Bronchocela* species contains copied sections from Boulenger (1885: 314, 316–317, approximately 26 lines) for *B. cristatella*.

In his comparison of the new species to other species of the genus *Bronchocela* the author also often refers to *B. moluccana* (Lesson, 1830) which is currently considered a synonym of *B. cristatella* (Kuhl, 1820). Interestingly he does not include *B. moluccana* in his species list (table at the end of his taxonomic section) although it is stated in his introduction to the genus that he regards *B. moluccana* "as being a separate species". We note that the original name given would be *Agama moluccana* Lesson, 1830 and the combination *B. moluccana* was only used by Peters (1867 as *Bronchocele*), Stoliczka (1870) and Peters & Doria (1878), all of which were in later publications considered to be *B. cristatella*. Theobald (1876) used the name *B. moluccana* in his *Reptiles of British India* for a specimen from the Nicobars as a synonym of *Pseudocalotes archiducissae* Fitzinger, 1860, which again turns out to be a synonym of *B. cristatella*. *Bronchocela moluccana* constitutes a *nomen oblitum* and resurrection should have been made clear with reference to the type species and holotype.

Furthermore Hoser refers several times to Java as the type locality for *B. cristatella*. In his original description Kuhl (1820) never mentions a type locality and ever since it has been unknown and never been restricted by any author (see for example Diong & Lim, 1998). One could argue that Hoser's statement "West Java (herein treated as terra typica)" is meant to be the newly defined type locality. This is an unfortunate choice under current conditions, as the actual phylogenetic status of the Javanese populations still needs further research as also pointed out by Hoser. Additionally Hoser does not refer to a particular specimen from his type locality and hence the restriction is not valid.

The genus *Phoxophrys* Hubrecht, 1881 is divided into three subgenera. In the introduction to the genus Hoser claims that "as there has never been a definition or diagnosis of *Pelturagonia*" Mocquard, 1890 he will "provide one herein for the first time". Hoser's diagnosis only comprises two characters while that of Mocquard (1890) is written in French, and longer with several characters. To diagnose the genus Hoser uses approximately 20 lines, all of which are copied from Inger (1960: 221) and include a comparison to *Japalura*, the genus several *Phoxophrys* species belonged to until Inger's revision.

Hoser's nominate subgenus is defined by a minimally rephrased diagnosis of *Phoxophrys tuberculata* Hubrecht, 1881 again taken from Inger (1960: 225, seven lines). The diagnosis of the subgenus to accommodate *P. cephalum* (Mocquard, 1890) only comprises two lines with two characters ("presence of nuchal crest … and an absence of a supraciliary spine"). The last subgenus only contains *P. spiniceps* Smith, 1925. This is defined within seven lines, all copied but slightly rearranged from Inger (1960: 224–225).

The next genus Hoser is concerned with comprises the lizards of the genus *Aphaniotis* Peters, 1864. The genus is divided into two subgenera on the basis of whether a "protrusion on the snout" is present or absent. The genus and nominate subgenus diagnoses are identical and each constitute a copy from Boulenger (1885: 274, four lines). The other subgenus is defined by approximately four additional lines that have been copied from the internet (www.ecologyasia.com) or a source that we have not identified.

The genus *Ptyctolaemus* Peters, 1864 currently consists of two species, which Hoser considers to be two subgenera. The nominate subgenus containing *P. gularis* Peter, 1864 is initially defined within 15 lines copied from Schulte et al. (2004: 230) followed by a comparison to *P. collicristatus* Schulte & Vindum, 2004 (Schulte et al. 2004) taken from the same source (five lines). The definition of the subgenus for *P. collicristatus* is precisely the other way round, i.e Hoser first uses the same five lines from the comparison betwee *P. gularis* and *P. collicristatus* to define the species and then the definition of the genus (all copied from Schulte et al. 2004: 230).

The genus *Salea* Gray, 1845 is currently considered to contain two species (see below) and one highly questionable species (*S. gularis* Blyth, 1854). In his introduction to the genus Hoser states that "neither the genus … or the subgenus being properly defined to date … this is done herein for the first time". He does however not present a single character to do so that has not been the result of a copying process from Boulenger (1885). Hoser breaks up the genus into two subgenera based on the respective descriptions of *S. horsfieldii* Gray, 1835 and *S. anamallayana* (Beddome, 1878) taken from Boulenger (1885: 251–252, 312–314) with 36 lines (annotated as "modified from Boulenger" but actually constituting a verbatim copy) and 22 lines, respectively. For the latter species he resurrects its original name proposed by Beddome (1878).

The last genus Hoser deals with in this part of the paper is *Draco* Linnaeus, 1758 which has been a matter of intensive morphological studies in the 1980s by Inger (1983) and Musters (1983). In recent years phylogenetic studies by McGuire & Alcala (2000), McGuire & Kiew

(2001) and McGuire et al. (2007) completed the picture. Hoser mainly uses these phylogenetic results and the tree of Pyron et al. (2013) to divide the genus into nine subgenera and copies their respective diagnoses from Boulenger (1885) or the morphology based publications mentioned before. Not a single new character is introduced by Hoser. Hoser's general description of the genus is given in 4.5 lines all taken from Boulenger (1885: 253). Only the phrase "much-produced" is replaced by "much-expanded".

The first new subgenus Hoser proposes serves to accommodate members of the *Draco lineatus* group (minus *D. lineatus* which is placed in its own monotypic subgenus, see below). Initially Hoser copies seven lines from McGuire et al. (2007: 181) to define the group including a statement related to a statistical analysis. However, Hoser does neither use nor refer to a statistical method in his section on methods. Subsequently he produces four lines form the same source to define his subgenus further (McGuire et al., 2007: 181) followed by a short description of *D. bimaculatus* Günther, 1864 taken from Muster (1983: 40) to distinguish this species from his subgenus. The last part of Hoser's diagnosis serves to separate *D. lineatus* Daudin, 1802 from his proposed subgenus of the remaining *lineatus* group species. This is done by copying the diagnosis comprising ten characters provided by McGuire et al. (2007: 199). At the end of this paragraph Hoser annotates "adapted from McGuire et al. (2007)" although he actually produces a complete verbatim copy from that source. This goes so far that Hoser even has the typographical error "posnuchal" [sic!] in the same place.

The new monotypic subgenus to accommodate *Draco bimaculatus* initially repeats the four lines taken from Musters (s. above) followed by a copy (ten lines) from McGuire et al. (l.c.) as given under the previously defined subgenus. Next Hoser uses again the "adapted" diagnosis for *D. lineatus* provided by McGuire et al. (2007: 199, 16 lines including typographical error, see above) and finally describes the species by copying Boulenger (1885:263, 19 lines) which again is annotated as having been "adapted" albeit constituting a word-for-word copy.

Draco modiglianii Vinciguerra, 1892 is placed by Hoser into its own new subgenus on the basis of a short diagnosis (3.5 lines) that has been copied from Musters (1983: 45).

Species related to *Draco blanfordii* Blanford, 1878 are combined in yet another new subgenus which he defines by copying three sets of characters originally from Boulenger (1885: 255, synopsis to the species, approximately nine lines). No other characters are presented.

Species related to *Draco maculatus* (Gray, 1845) are contained in a new subgenus that is entirely defined by 18 lines coming from Boulenger (1885: 262). The nominate subgenus is diagnosed in approximately three lines copied from Inger (1983: 17).

Then Hoser defines *Draco lineatus* Daudin, 1802 in pretty much the same way he did to diagnose the *lineatus*-group (s. above). Initially he uses McGuire et al. (l.c.) to define the *lineatus*-group (approximately nine lines copied); this is followed by separating *D. bimaculatus* from that group and the proposed subgenus by copying Musters (1983: 40, 4.5 lines). Finally Hoser reproduces the full set of characters as given by McGuire et al. (2007: 199) for the species annotated as adapted but actually copied. For this subgenus Hoser resurrects an old available name from Fitzinger (1843).

Species related to *Draco fimbriatus* Kuhl, 1820 are placed into a subgenus for which another name proposed by Fitzinger (l.c.) is resurrected. The subgenus is defined in approximately three lines and subsequently separated from *D. maculatus* (again three lines), all copied from Boulenger (1885: 254–255).

The last subgenus Hoser erects serves to accommodate the Indian species *Draco dussumieri* Duméril & Bibron, 1837. To name the subgenus Hoser resurrects another of Fitzinger's names (l.c.). The diagnosis consists of four lines taken from Boulenger's synopsis (1885: 255) followed by approximately 17 lines of description copied from the same source (Boulenger 1885: 268).

After having defined his genera and subgenera Hoser endeavours to divide the subfamily into tribes and subtribes. Hoser proposes ten tribes and six subtribes, which will be numbered numerically in the following in order to prevent accidental validation; genus names are given here in their currently accepted form.

Tribe 1 only contains lizards of the genus *Draco*. Tribe 2 contains the genera *Japalura* [in part] and *Pseudocalotes* (subtribe 2.1), *Sitana* and *Otocryptis* (subtribe 2.2), *Acanthosaura* and *Oriocalotes* (subtribe 2.3) and *Salea* (subtribe 2.4). Tribe 3 only contains *Calotes*. Tribe 4 is represented by *Gonocephalus robinsonii* and *Japalura polygonata*. Tribe 5 consists of *Ceratophora*, *Cophotis*, *Pseudocophotis* and *Lyriocephalus* (subtribe 5.1), *Gonocephalus mjobergi* (subtribe 5.2), *Gonocephalus*, *Bronchocela*, *Complicitus*, *Hypsicalotes*, *Coryphophylax* and *Aphaniotis* (subtribe 5.3). Tribe 6 comprises *Japalura* [in part, including *Oriotiaris*] and *Ptyctolaemus*. The remaining tribes contain a single genus each: Tribe 7 *Lophocalotes*, Tribe 8 *Phoxophrys*, Tribe 9 *Mantheyus* and Tribe 10 *Dendragama.*

The nodes produced in Pyron et al. (2013) are given in the following as A–H with corresponding tribe numbers (as given above) from Hoser in brackets: A(1) – *Draco*, B(2) – *Japalura* Eastern clade, *Pseudocalotes*, *Sitana*, *Otocryptis*, *Acanthosaura*, *Salea*, C(3) – *Calotes*, D(4) – *Japalura polygonata* & *Gonocephalus robinsonii*, E(5) – *Ceratophora*, *Cophotis*, *Lyriocephalus*, *Gonocephalus*, *Bronchocela*, *Coryphophylax*, *Aphaniotis*, F(6) – *Ptyctolaemus* and *Japalura variegata* clade, G(8) – *Phoxophrys* and H(9) – *Mantheyus.*

As can be seen Hoser's taxonomic scheme essentially reproduces the clades resulting from the phylogenetic analysis by Pyron et al. (2013). His subtribes can be derived in a similar way. *Lophocalotes* (Hoser's Tribe 7) and *Dendragama* (Hoser's Tribe 10) are not included in Pyron's analysis nor are *Harpesaurus*, *Thaumatorhynchus*, and *Psammophilus*. The first two are recognized by Hoser in their own monotypic tribes, the other three are not dealt with at all. Other genera also not included in Pyron et al. (l.c.) such as *Oriocalotes*, *Hypsicalotes*, and *Complicitus* are assigned to a tribe but without giving a reason for doing so. However, with a bit of nomenclatural research one could find possible reasons for his groupings: *Oriocalotes paulus* was considered by Boulenger as *Acanthosaura minor*, hence Hoser's pairing of these two genera. In his introductory sentence to the genus *Complicitus* he states that it was "formerly placed in *Bronchocela*". In the same publication (Malkmus 1994, a paper written in German) *Hypsicalotes* is also considered to be a member of the genus *Bronchocela*. This is presumably Hoser's reasoning behind grouping these two genera in the same tribe along with *Bronchocela* and several other species from the same node in Pyron et al. (l.c.). Had Hoser decided to follow the majority of earlier publications, all of which are cited by him, he would likely have included these two genera in the tribe containing *Calotes*, their original genus name.

Hoser's division of the subfamily Draconinae can only be understood and followed if Pyron's paper is at hand for comparison. His classification scheme is poor-quality if not worthless as most tribes and subtribes are not diagnosed by shared characters but only through their content. In Hoser's words:"…tribe is best defined by diagnosis of the component genera" or a similar wording. Such a definition may comprise the character sets of 13 genera as given in the first section of his paper where the genera are defined. All diagnoses are copied and no additional data or characters are given. Some genera were not defined in their own right in Hoser's first section of the paper. These genera are therefore diagnosed by him as a character set defining a tribe or subtribe. In the following we will briefly analyze these additional diagnoses:

Hypsicalotes Denzer & Manthey, 2000 is diagnosed by repeating entirely the diagnosis including comparisons to other genera as given in Denzer & Manthey (2000, approximately 60 lines). *Coryphophylax* Fitzinger, 1869 is defined in the space of six lines copied from Boulenger (1885: 282). *Cophotis* Peters, 1861 is diagnosed by copying Boulenger (1885: 251–252, three lines; 275, three lines). *Pseudocophotis* Manthey in Manthey & Grossmann, 1997 is a copy of Boulenger's description of *Cophotis sumatrana* (= *Pseudocophotis sumatrana*). *Complicitus* Manthey in Manthey & Grossmann, 1997 is defined in approximately two lines taken from the Reptile Database website (primary source not identified). *Lophocalotes* Günther, 1872 is diagnosed in approximately eight lines of which four lines each are from Boulenger (1885: 251) and de Rooij (1915: 116) or partially from Hallermann (2004). The genus *Phoxophrys* Hubrecht, 1881 is defined for a second time but this time using Boulenger (1885: 251, 280, six lines copied) instead of using Inger (1960). The definition of *Dendragama* Doria, 1888 has been copied (approximately three lines) from de Rooij (1915: 117–118).

Summary Section A

Apart from some minor alterations the phylogentic tree published by Pyron et al. (2013) serves as Hoser's main basis for his classification scheme of the Draconinae.

In our analysis of Hoser's proposed taxonomy for the subfamily Draconinae most characters were identified and can be attributed to other sources. Hoser gives his diagnoses in the space of 2430 lines where 1884 lines constitute the actual characters of which 1560 lines have been identified as identical copies. If only diagnostic characters are taken into account approximately 83% are a copy and if the full diagnoses are considered this percentage still comes to approximately 64%. If the full paper is taken into account (7140 lines, estimated) the copied text still amounts to approximately 22%. At the end of his paper Hoser cites several hundred references in a space of close to 16 pages. However, according to our analysis he only used approximately 30 of those to produce his proposed taxonomy, the bibliography of which could probably have been printed in the space of two pages. If this is taken into account the percentage of copied text in relation to the full paper rises by yet another 5%.

Hoser's main source for descriptive characters was Boulenger (1885). Additionally he copied sections from Inger (1960) for *Phoxophrys*, Denzer & Manthey (2000) for *Hypsicalotes*, Hallermann (2004) for *Bronchocela*, McGuire et al. (2007) for *Draco*, Denzer & Manthey (2009) for *Gonocephalus*, Mahony (2009) for *Japalura*, Zug et al. (2006), Krishnan (2008) and Hallermann (2000) for *Calotes*, Harikrishnan & Vasudevan (2013) for *Pseudocalotes,* Pethiyagoda & Manamendra-Arachchi (1998) for *Ceratophora* and Schulte et al. (2004) for *Ptyctolaemus*. Several genera such as *Harpesaurus*, *Thaumatorhynchus*, and *Psammophilus* are not treated at all.

B) Hoser (2013) on Amphibolurinae

We note that the manuscript on Amphibolurinae was received by *AJH* on 20 July 2013, accepted for publication on 4 October 2013, and published on 20 October 2013. However, a tax invoice printed at the end of the publication (p. 36) states that the journal was printed on 3 October 2013, implying printed copies may have existed before the paper was accepted.

The paper comprises the following sections or headings: *Title*, *Abstract* (including *Keywords*), *Introduction*, followed by the description of two genera and seven tribes, *References Cited*, and a statement about *Conflict of Interest*. An explicit section for Materials is missing (but see below) and one has to assume that the description of the new taxa constitutes a combined Results/Discussion/Conclusion section.

The introductory part of a publication typically includes a brief overview and often the author's motivation for writing the paper, as well as his ideas about the subject. In standard practice, reviewers of manuscripts in mainstream journals would not spend much effort in correcting this part unless false statements are presented. However, in the case of this particular introduction, it is instructive for a better understanding of the broader picture of Hoser's works to mention several paragraphs.

Hoser begins by providing a reason for why the Australasian Amphibolurinae Wagler, 1830 are so well studied. According to Hoser this "has arisen due to a combination of circumstances **relatively unusual** to Australia" (emphasis added). The two factors alluded to are a "stable political and economic situation" including a transport infrastructure that facilitates access to even the most remote parts and "well-funded government paid herpetologists and relatively wealthy … private herpetologists … able to travel to the most remote parts of the continent…".

A significant portion of the *Introduction* deals with the publications by Wells and Wellington (1983, 1985), which are considered highly controversial papers in their own right and still do not find full acceptance within the herpetological community. One part of a paragraph reads as follows (Hoser 2013: 34): "I have found myself resurrecting names proposed by earlier authors. This includes a number of effectively unused Wells and Wellington names such as *Intellagama* Wells & Wellington, 1985, *Gowidon* Wells & Wellington, 1983 …" However, at the time of this paper's publication (October 2013) the genus name *Intellagama* had already been validated by Amey et al. (2012) and the genus name *Gowidon* in the combination *G. longirostris* (Boulenger, 1883) was made available by Melville et al. (2011). Both publications were not cited by Hoser (2013).

One of the paragraphs in Hoser's *Introduction* would never pass standard review of any formal publication in science and would be removed by editors as it is against ethical standards of publication. A group of herpetologists (one named in particular) that is highly critical of Hoser's papers is called "a mob of criminals and ratbags" (Hoser 2013: 34).

At the end of the *Introduction*, Hoser uncritically lists 14 publications, five of which are his own, "and sources cited therein" that apparently constitute the source material for his research. However, major publications on Australian agamids relevant to taxonomy and nomenclature, such as Melville et al. (2011), Hugall & Lee (2004), Hugall et al. (2008), Schulte et al. (2003), or Macey et al. (2000a,b) are not mentioned at all and the reader would need to refer to the few cited papers and their bibliographies to determine how Hoser derived some of his ideas. While this paragraph could be regarded as a Materials section, it should be noted that not a single museum specimen is referenced, nor is there any mention that museum material was examined. Earlier in the *Introduction* Hoser (2013: 33) notes: "In terms of the materials and methods, this was based on my own field and lab work involving most species as well as a review of the relevant literature spanning the last 200 years." With respect to "lab work," the reader does not get any further explanation of what this entailed, making the process non-transparent and non-reproducible. The list of references given in the *References Cited* section of the paper comprises only 16 citations, five of which are Hoser's own publications. Of those, at least Hoser (1998) on *Acanthophis* and Hoser (2012) on *Afronaja* are entirely irrelevant to agamid lizard taxonomy.

Only Joger (1991) and Pyron et al. (2013) are referenced as publications that include original molecular phylogenetic research that is indispensible to Hoser's arguments. However, Joger's paper (l.c.) only includes *Amphibolurus vitticeps* (Ahl, 1926) (= *Pogona vitticeps*) and *Physignathus temporalis* (Günther, 1867) (= *Lophognathus temporalis*) in the analysis, making it of only peripheral interest for a detailed phylogenetic analysis of Australian taxa (Joger 1991, Material Examined). Joger (1991: 619) even notes: "Because of the lack of antisera for East Asian and Australian agamids, the position of their three lineages – *Amphibolurus*/*Physignathus*, *Calotes*/*Acanthosaura*, and *Gonocephalus* – relative to each other could not be determined." It is important to note that Joger did not study the genera *Physignathus* Cuvier, 1829 and *Amphibolurus* Wagler, 1830, but two specimens of populations that were considered members of these genera at that time, but are assigned to different genera today. Additionally, no nomenclatural decisions were proposed by Joger (l.c.).

It therefore stands to reason that Pyron et al. (2013) serves as the basis for Hoser's taxonomic and nomenclatural proposals. This becomes particularly obvious in the grouping of *Moloch* Gray, 1841 and *Chelosania* Gray, 1845 within a single tribe. Without recent molecular phylogenies it is unlikely that any morphologically-oriented herpetologist would group a thorny devil (whose vernacular name illustrates a key aspect of the species' scale morphology) with a lizard that has a completely homogeneous dorsal scalation. The phylogeny of Pyron et al. (2013) is also reflected in acknowledging the difference between *Physignathus* and *Intellagama*, the splitting of *Hypsilurus* into several genera, the erection of a tribe for the genus *Ctenophorus*, and combining *Amphibolurus*, *Chlamydosaurus*, *Diporiphora*, *Gowidon* (*Lophognathus*), *Pog-*

ona, *Rankinia*, and *Tympanocryptis* within one tribe, albeit using a different nomenclature.

The *Introduction* is followed by a section that serves to erect two new genera and seven tribes. New tribes are presented in random order without presenting necessary information on possible phylogenetic relationships. Our analysis will mainly follow Hoser's order but for reasons of clarity the tribe containing the genera related to *Amphibolurus* and the tribe containing all *Ctenophorus* will be dealt with last.

The first genus described in the paper is meant to accommodate only *Diporiphora superba* Storr, 1974. The actual diagnostic characters account for approximately nine lines of text, of which eight can be accounted for in Cogger (1983: 238, key leading to *D. superba*; 1983: 243, description of *D. superba*). Differences include changing "gular fold absent" to "no gular fold" and replacing the % sign by "percent," as well as replacing the numeric "4" by the word "four." The unaccounted text consists mainly of introduced verbs and a slightly modified description of the colouration.

The second genus described deals with *Hypsilurus spinipes* (Duméril & Bibron, 1851). The diagnostic character section accounts for approximately 12 lines and is annotated as "adapted from Cogger, 2000." About 11 lines are the result of directly repeating Cogger's description of *H. spinipes* (Cogger 1983: 245–46, as *Gonocephalus spinipes*) and the only differences are the introduction of a few verbs and conjunctions.

The new genus containing *Hypsilurus spinipes* is subsequently placed into a newly erected tribe that additionally contains *Tiaris* Duméril & Bibron, 1837 (see below). The diagnosis for the tribe contains two sets of characters. The first part (ca. seven lines) is a copy of Cogger's key leading to *Hypsilurus* (Cogger 1983: 217, as *Gonocephalus*) apart from a few introduced verbs and conjunctions (one line). The second part (eight lines) states the characters shared by *Hypsilurus* species and is a copy (six lines) of the genus diagnosis given by Manthey & Denzer (2006). The latter paper is not cited, and the diagnosis was most probably retrieved from the Reptile Database (Uetz & Hošek 2015), where it is publicly available (cited, and with approval of the authors). The genus *Tiaris* is not characterized at all in Hoser's paper, nor is the reader informed which species it contains. In Hoser's paper the name stands on its own and is therefore a *nomen nudum* according to the *Code*. It should also be noted that *Tiaris* Duméril & Bibron, 1837 is not available for any agamid genus as it is preoccupied by *Tiaris* Swainson, 1827 (Aves, Passeriformes) [see Manthey & Denzer (2006)].

According to Hoser an agamid genus *Tiaris* is of Australian origin and "the only genus it is likely to be confused with" is the one newly erected for *Hypsilurus spinipes*. The only other *Hypsilurus* species in Australia that Hoser could refer to is *H. boydii* (MacLeay, 1884), albeit that it is actually quite difficult to confuse these two species. *Hypsilurus boydii* is known from older literature as *Tiaris boydii* (e.g., MacLeay 1884). Hence, we assume that Hoser meant to include this species in the same tribe as *H. spinipes*. However, *H. boydii* is morphologically (Manthey & Denzer 2006) and genetically (Pyron et al. 2013) closely related to *H. dilophus* (Duméril & Bibron, 1837), which Hoser places into a different tribe.

The next tribe is erected to accommodate the genus *Hypsilurus*, assigning *Lophura* (*Hypsilurus*) *godeffroyi* Peters, 1867 as the terminal taxon. Hoser's introduction to the tribe starts with the sentence "Currently most widely known as *Hypsilurus dilophus* (Duméril & Bibron, 1837)." It is not clear whether Hoser here expresses his view that *H. godeffroyi* (a well-defined and valid species) is identical to (conspecific with) *H. dilophus*. His statement is even more confusing considering that *H. dilophus* is actually the type species of the genus *Tiaris* Duméril & Bibron, 1837, a genus he assigned a paragraph earlier to a different tribe (for synonymy of *Hypsilurus* see Manthey & Denzer 2006). Additionally there exist no objective reasons to combine *H. dilophus* and *H. godeffroyi* into one group. Morphologically, they are very different species that were even placed into different species groups by Manthey & Denzer (2006). In his genus description to accommodate *H. spinipes*, Hoser states that *Tiaris* (*nomen nudum*, see above) and all *Hypsilurus* species have a "longitudinal row of grossly enlarged scales on the throat." This is actually a character used by Cogger (1983) to differentiate between *H. spinipes* and *H. boydii*, which should read, "median longitudinal line of … similar to those in the nuchal crest." The statement holds true if only Australian species are considered, as is the case with Cogger (l.c.), but when including taxa outside of Australia, as Hoser's analysis does, it is false, as most species of *Hypsilurus* outside Australia actually lack a median line of enlarged scales on the gular pouch. These are only well developed in *H. boydii* and *H. dilophus*, and to a lesser extent in *H. hikidanus* Manthey & Denzer, 2006. As already pointed out by Manthey & Denzer (2006), *H. dilophus*, *H. boydii*, and *H. spinipes* may be considered as a species group, and if considered as a separate genus only the name *Lophosaurus* Fitzinger, 1843 would be available but not *Tiaris*. The diagnostic character section for *Hypsilurus* comprises 15 lines of which 13 lines are copied from Cogger (l.c.) and Manthey & Denzer (2006).

Subsequently, Hoser deals with the water dragons from Australia and Southeast Asia. The relationship, biogeography, and nomenclature of *Physignathus cocincinus* Cuvier, 1829 and *Intellagama lesueurii* (Gray, 1831) has been a matter of intense discussion, and since the advent of molecular phylogeny there have been several publications to address the issues (e.g., Schulte et al. 2003, Macey et al. 2000a,b). Still Hoser makes no mention of this and erects

two new tribes. His claim to have resurrected the genus name *Intellagama* has already been dealt with (see above). The diagnostic characters to define the tribe for *I. lesueurii* account for ca. five lines of text, three of which are copied from Cogger's key (Cogger 1983: 217). The remaining part of the description deals with colouration, but not as one would expect, with a description of the colouration of *I. lesueurii*. Hoser instead merely states that the colouration is not that of *P. cocincinus*.

The tribe containing the latter species is again initially diagnosed via Cogger's key (l.c.), with three lines out of four being copied. The remaining part of the diagnosis deals with the colouration of *Physignathus cocincinus*. Apart from the dorsal ground colour (one line) the patterns and colourations (three lines) were copied from Wikipedia, with no primary source identifiable. The Wikipedia page already provided this description of the colouration in 2012 (accessed August 2014, file history checked for December 2012), i.e. before Hoser's paper was published.

Next Hoser introduces a tribe to accommodate the genera *Moloch* and *Chelosania*. The two diagnostic sections consist of two lines and four lines, respectively, of which approximately four lines are copied text (Cogger 1983: 217).

Another tribe is erected to accommodate the genus *Ctenophorus*. The diagnostic characters are presented in roughly sixteen lines, ten of which are copied from Cogger (1983) and three from Cogger (1993). One set of characters regarding the supralabial scales could not be accounted for and is potentially the only part of an original description in the entire paper. From the lack of methodology, it is not possible to determine how these observations were made or which specimens were used, rendering the data non-reproducible. Furthermore, the copied part contains several mistakes that need to be addressed.

The diagnosis for the new tribe containing the genus *Ctenophorus* is at best confusing, and perhaps of no taxonomic value entirely. Part of Hoser's definition reads as follows (emphasis added): "nuchal crest and/or series of enlarged keeled vertebral scales present or absent and if **absent present** along at least the anterior two thirds of the **body; enlarged** strongly keeled or spinose scales are present elsewhere on the dorsum." The diagnostic characters are identical those used in Cogger's key to the genera (1983: 217), apart from the conflicting phrase "absent present" and the placement of the semicolon. The use of both "absent" and "present" in close combination makes it unclear how this character is to be scored. In common usage, placing a semicolon will not change a diagnosis significantly. However, in this case only the part directly preceding the semicolon relates to the character of "enlarged keeled vertebral scales present or absent". The character after the semicolon "enlarged strongly keeled scales … present … on the dorsum" stands on its own. This way all *Ctenophorus* without this character are excluded from the genus! Cogger (1983: 217) included this particular set of characters as a full statement in the diagnosis for the genus *Amphibolurus*. There it reads, "nuchal crest and/or vertebral keel may be present, but if the latter is present on at least the anterior two-thirds of the body then enlarged, strongly-keeled or spinose scales are present elsewhere on the dorsum", giving it a completely different meaning. It should be noted that a key matching this part of Hoser's diagnosis, including the (wrong) placement of the semicolon, can be found in another earlier publication (Cogger 1993: 163, or in the online version on page 10, character 9a). A further character to define the tribe presented by Hoser is described on the basis of the online publication (page 11) but introducing yet another mistake. Hoser's character reads: "a row of enlarged scales from below the eye to above the eye" instead of "to above the ear"!

The genus- and species-richest tribe introduced in the paper contains the genera *Amphibolurus*, *Chlamydosaurus*, *Caimanops*, *Cryptagama*, *Diporiphora*, *Gowidon* (*Lophognathus*), *Pogona*, *Rankinia*, and *Tymapnocryptis*, as currently accepted by most Australian herpetologists (here listed according to Cogger 2014; it should be noted that *Gowidon* is not yet generally accepted). However, according to Hoser's compilation the genus *Lophognathus* no longer exists. Hoser instead uses *Gowidon*, a name available for *L. longirostris*, but ignores *L. burnsi* Wells & Wellington, 1985, *L. gilberti* Gray, 1842, and *L. temporalis* (Günther, 1867). For this reason the reader has to assume that Hoser considers these species as congeneric or even conspecific. However, in this case the name *Gowidon* would not be available since the genus name *Lophognathus* has nomenclatural priority over it, with *L. gilberti* being the type species of the genus.

If Hoser had been consistent in following the data of Pyron et al. (2013), then *Tympanocryptis* Peters, 1863 should also be a member of this tribe. However, Hoser does not include it here or in any other tribe, nor does he use a different taxonomy to pinpoint where the species of this genus might be grouped, perhaps as part of one of the other genera used in the revised classification scheme. It appears that, just as some members of *Lophognathus*, the genus *Tympanocryptis* was simply disregarded or forgotten. *Tympanocryptis* is an available name that should be used, the type species being *T. lineata* Peters, 1863.

Hoser recognizes *Caimanops* Storr, 1974 and two genera proposed by Wells & Wellington (1983, 1985) containing *Diporiphora* species. One of these genera was erected to accommodate *D. albilabris albilabris* Storr, 1974 and *D. albilabris sorbia* Storr, 1974. The second was erected for *D. linga* Houston, 1977 and *D. winneckei* Lucas & Frost, 1896. We assume that Hoser resurrects these genera from their synonymy with *Diporiphora*, albeit without mentioning it specifically or giving a reason for

doing so. These genera were formally synonymized with *Diporiphora* by Doughty et al. (2012), owing to their close phylogenetic relationship, and were included by Pyron et al. (l.c.) under *Diporiphora*. It appears that Hoser overlooked the publication by Doughty et al. (2012). *Caimanops* has so far been considered a monotypic genus, with *C. amphiboluroides* as the sole species. If Hoser had properly followed Pyron et al. (l.c.), he should also have assigned *D. australis* to *Caimanops* as these two species form a clade.

The diagnostic characters employed by Hoser to group the above genera into a new tribe are as follows: Initially he singles out *Chlamydosaurus* by repeating Cogger (1983 two out of two lines copied) but introducing a mistake. Hoser's character reads, "a large loose frill or skin around the neck" but it should read, "… frill of skin …". Hoser then proceeds to define the general characters of this diverse group (Cogger 1983; four out of four lines copied). In his last part of defining the tribe he excludes the genus *Ctenophorus* in an identical way as he defined the tribe containing the genus, including all the mistakes discussed above. Overall Hoser's diagnostic character section of this tribe comes to 22 lines of which 16 lines are a result of copying.

Summary Section B

Hoser's classification scheme for amphibolurine lizards mostly reflects the nodes in the phylogenetic tree published by Pyron et al. (2013). Additionally several genera proposed in the highly controversial papers by Wells & Wellington (1983, 1985) are accepted as valid.

Hoser gives his diagnoses in the space of 153 lines, of which 121 lines constitute the actual characters, with 100 lines clearly identifiable as copied. If only diagnostic characters are taken into account this amounts to 82% copied material, with the full diagnoses included it is still 65%. If the full paper is taken into account (438 lines) the copied text amounts to 23%.

All but a single character can be identified and attributed to secondary sources (Cogger 1983, 2000; Manthey & Denzer 2006; Anonymous on Wikipedia; Uetz & Hošek 2015).

Most characters used to describe genera are taken directly from Cogger (1983 or subsequent editions). Several important publications on Australian agamid lizards such as Melville et al. (2011), Hugall & Lee (2004), Hugall et al. (2008), Schulte et al. (2003), or Macey et al. (2000a,b) have been omitted. The genera *Lophognathus* and *Tympanocryptis* are not treated at all.

C) Hoser (2012a) on *Laudakia* Gray, 1845

The manuscript was received on 13 March 2012, accepted on 8 April 2012 and the paper was published on 30 June 2012. Hoser's paper is presented in the following way: *Abstract* (including *Keywords*), *Introduction*, description of taxa, and *References Cited*. The second to fifth paragraphs of the *Introduction*, describing the general appearance and behaviour of the group, contain 13 lines of copied material from an online source (www.sauria.co.uk). The rest of the *Introduction* deals with the nomenclature and phylogeny of *Laudakia* Gray, 1845 and *Phrynocephalus* Kaup, 1825. His nomenclatural arguments refer mainly to Henle (1995) and are misinterpreted (see comments for the *stellio* group).

Hoser's "five-way division" of *Laudakia* Gray, 1845 mainly reflects the phylogenetic schemes published by Macey et al. (1998, 2000b, 2006), who identified nodes supporting a *L. tuberculata* group, a *L. caucasia* group with *L. lehmanni* as the sister taxon (proposed as a new subgenus by Hoser), as well as nodes supporting the monophyly of *L. stellio* (Linnaeus, 1758) and *L. sacra* (Smith, 1935). Hoser's fifth group comprises *Phrynocephalus* Kaup, 1825, a genus of lizards that has never been in the synonymy of *Laudakia*. Macey et al. (2000b) found *Phrynocephalus* to be a sister taxon to both the clade containing the *L. caucasia* group and *L. stellio*. However, in a later publication by Melville et al. (2009), the monophyly of the genus *Laudakia* was confirmed and *Phrynocephalus* emerged as the sister taxon to the whole clade. Apparently, Hoser and his supposed reviewers overlooked this important publication, which is not cited in his bibliography.

The first genus Hoser deals with is that of *Phrynocephalus* Kaup, 1825, which he considers "similar in most respects to *Laudakia* sensu lato" (Hoser 2012: 18), a statement most herpetologists would disagree with. Hoser does not present a meaningful definition of the genus apart from "lacking of an obvious tympanum" to distinguish *Phrynocephalus* from *Laudakia* and a "dorsoventrally depressed" body to distinguish it "from all other other Agamids in the region where these groups of lizards occur." This entire diagnosis holds no definitive value as there are other agamid genera in the area under consideration that have a dorsoventrally depressed body shape (e.g., *Brachysaura* Blyth, 1856, *Bufoniceps* Arnold, 1992, and *Trapelus* Cuvier, 1829). Another interesting fact is that Hoser only recognizes 26 species within the genus *Phrynocephalus* while the actual number had already surpassed 40 species by the time his paper was published. This is certainly something any expert reviewer would have been able to point out, even by a simple search of the Reptile Database (Uetz & Hošek 2015).

Hoser moves on to define what he considers to be the actual genus *Laudakia*. This is represented by the *tuber-*

culata group and hence *L. tuberculata* (Gray, 1827) becomes the type species. Initially he uses tympanum presence and body shape to distinguish it from *Phrynocephalus* and other genera of agamid lizards in the region. This is followed by a short description (eight lines) mostly copied from a key to the species of agamid lizards of Pakistan (six lines; Khan 2002: 100 & 101). The same key is available on the Internet as part of Khan's undated eBook *Herpetology of Pakistan*. Neither of these two publications are cited by Hoser! Based on the idiosyncratic character "fifth toe extends beyond second" we have no doubts that Khan's publication is the source; other authors make a comparison to the first toe. Hoser's further characters include the dentition and the number of whorls in each tail segment. Both characters are from Baig (1992) but the writing has been sufficiently altered that they do not constitute copied material. The entire diagnosis of the genus comprises 32 lines (18 lines of diagnostic characters) of which six lines are copied, presumably from Khan (2002).

The next genus proposed by Hoser serves to accommodate the *Laudakia caucasia* (now *Paralaudakia caucasia*, see below) group. Up to this point we have mostly abstained from judging Hoser's diagnoses but the poor quality of this one requires analysis. It begins with an essentially copied general diagnosis from earlier in the paper, but "excluding those genera formerly placed within *Laudakia* sensu lato" by which Hoser means the other genera he proposed (see above). Subsequently, he copies from Khan (2002): "tympanum is large,… fifth toe extends beyond second; caudal scales in distinct annuli," which is unfortunately a character set that still defines the entire genus. Up to this point, no character has been listed that could be used to define the new genus. Next, Hoser states that "the scales of dorsal rows are smooth," "the premaxilla has two teeth in the [new] genus versus three in *Laudakia* [= *L. tuberculata* group]," and "lizards in this [new] genus have 14–15 molars, versus 14–15 [sic!] in *Laudakia*." The author then once more repeats the general paragraph to differentiate *Phrynocephalus* and other agamids. He then separates his new genus from *L. sacra* by providing a full description of this species that is identical to the one found in Ananjeva et al. (1990). To summarize this for clarity: the only diagnostic characters presented to define his new genus –other than those characters which are common to all genera concerned– are "scales of dorsal rows are smooth," "premaxilla has two teeth," and presumably the number of molar teeth.

The definition for the new genus is, unfortunately for Hoser, not cohesive because the vertebral scales of *Paralaudakia caucasia* (Eichwald, 1831), the proposed type species of the new genus, are actually keeled and those of *P. himalayana* (Steindachner, 1867) and *P. badakhshana* (Anderson & Leviton, 1969) are smooth (Boulenger 1885; Khan 2002; Baig et al. 2012). We are not aware – and it is outside the scope of this paper to investigate further – how many teeth are present in the premaxilla and how many molars the other genera possess, in order to verify or falsify these two characters, nor is Hoser apparently. To our knowledge there are no publications dealing with the dentition of all genera in question. In total his diagnosis of this genus comprises about 56 lines, of which 27 are copied from Ananjeva et al. (1990). Three lines describing diagnostic characters are taken from Baig (1992) and Khan (2002), but not copied directly. Baig et al. (2012) established the genus *Paralaudakia* Baig, Wagner, Ananjeva & Böhme, 2012 to accommodate species related to *caucasia* and *himalayana* as well as *lehmanni* and *stoliczkana*.

For the *Laudakia stellio* (now *Stellagama stellio*, see below) species group, which Hoser considers to be monotypic, the author resurrects *Plocederma* Blyth, 1854. This can only be explained by misinterpreting Henle (1995) who proposed to use this genus name for the *stellio* group, which he considered to comprise *L. stellio, L. caucasia, L. erythrogastra, L. himalayana, L. lehmanni, L. nupta*, and *L. melanura*. The type species for the genus *Plocederma* is *L. melanura*. Only if this species were included in Hoser's *stellio* group (which it is not) would the name be available for the group. Because the *stellio* group as it is considered nowadays (i.e. monotypic) did not have any previous available name disposable, Baig et al. (2012) established the name *Stellagama* Baig, Wagner, Ananjeva & Böhme, 2012.

The new genus to accommodate *Stellagama stellio* is initially only defined by repeating his general description (two characters: "distinct tympanum" and "dorsoventrally depressed" body) followed by two lines taken from Khan (2002) and a description of "*Laudakia stellio*" (approximately 14 lines, all copied) taken from a website (Göçmen, www.bayramgocmen.com/album/picture.php?/1012/category/345, accessed September 2014). The full diagnosis comprises 26 lines (18 lines of diagnostic characters), of which 16 are copied.

To define his newly proposed monotypic subgenus to accommodate *Laudakia lehmanni* (Nikolsky, 1896), Hoser presents diagnostic characters in the space of approximately 38 lines, all of which come straight from Baig's description (1992) of *L. lehmanni*. The order of characters is slightly different from the original and in a few places verbs or conjunctions have been added. The diagnosis is followed by distributional data and habitat description, which constitutes (apart from one sentence) a copy of the text produced on the IUCN RedList webpage (six lines out of seven copied). The whole diagnosis comprises 42 lines of which 38 lines constitute diagnostic characters all of which are a copy from Baig (1992).

Hoser lists four papers by Baig and co-authors in the *References Cited* section, but none of these contains a description of *L. lehmanni* (now *Paralaudakia lehmanni*, see

below). A detailed description of *P. lehmanni* that is very similar to the one used by Hoser – but with characters in a different order – was first given in Baig's PhD thesis (Baig, 1992: 130 & 132, not cited by Hoser) which was completed under the supervision of WB. Since Baig's thesis has to be considered unpublished, Böhme and coworkers (Baig et al. 2012) posthumously published a paper based on the thesis to preserve Baig's extensive taxonomic work and to make it available for scientists working on this subject. In the latter publication Baig's description is repeated with minor changes and with pretty much the same wording seen in Hoser (2012a). Baig et al. (2012) was published in print on 18 July 2012 and Hoser (2012a) was published in print 30 June 2012. Both papers were accepted for publication by the respective journals in April 2012. We also note that Baig et al. (2012) was made available in advance online on the publisher's website on 6 July 2012, appearing a week after Hoser's publication. The most likely way by which Hoser would have been able to retrieve Baig's text would have been by downloading the thesis from a governmental website in Pakistan (Pakistan Research Repository, http://eprints.hec.gov.pk/2407/1/2262.htm). Although it is difficult to proof, but based on the exact wording, we are convinced that Baig's thesis was available to Hoser, who did not consider it necessary to reference it. However, even if not published a PhD thesis constitutes intellectual property belonging to the candidate and his thesis supervisor. In any case the precise repetition of wording from a thesis without appropriate clarification, attribution and referencing constitutes a violation of authorship rights. Any use of a verbatim copy of excerpts from a thesis needs permission by either the author, his thesis supervisor or the university department where the candidate studied for the degree. However, a reader who does not know about Baig's thesis might suppose that Hoser's diagnosis has precedence, with Baig et al. (2012) copying Hoser's ideas and wording when the opposite is the case. In this instance, Hoser clearly uses the intellectual property of another and passes it off as his own. Such behaviour would even be seen as plagiarism if Hoser obtained the description from a third source, which we have not identified. In a recent paper Hoser (2015) even claims priority and that "they [Baig et al. (2012)] did however remanufacture theirs [morphological evidence] as "new" data, which in itself is fraudulent". Hoser (l.c.) clearly states that data were available from earlier studies but again does not disclose or cite the source. Not only did Hoser plagiarize Baig (1992), he even considers his actions as justifiable and additionally accuses the true original author of fraudulent behaviour!

The last genus Hoser proposes is monotypic for *Laudakia sacra* (Smith, 1935). His diagnosis is given within 27 lines, of which 25 are a direct copy from the description of *L. sacra* by Ananjeva et al. (1990; see also Uetz & Hošek 2015) and two lines are copied from Khan (2002). The only two other characters are those used previously ("a distinct tympanum" and "the body is dorsolaterally depressed"), repeating nearly the entire general paragraph for the fifth time. The diagnosis of this genus is given in 33 lines, with 30 lines presenting the actual diagnostic characters, of which 27 lines are copied.

Summary Section C

The taxonomic basis for Hoser's proposals on *Laudakia* can be found in their entirety in Macey et al. (1998, 2000b, 2006). Most of Hoser's proposed classification additionally reflects nodes in the phylogeny published by Pyron et al. (2013).

In total, Hoser's paper on *Laudakia* comprises an estimated 980 lines, of which 420 lines constitute his *References Cited* section (560 lines pure text including *Title* and *Abstract*). We would like to mention that already his introductory part contains at least 13 lines that can be found on websites (not taken into account here as copied text) and that we further identified several diagnostic characters Hoser used but without copying directly. His diagnoses come to 180 lines of which 148 lines constitute diagnostic characters. With respect to the latter we found that 114 lines (77%) were copied from previously published research papers or reviews. Hoser's main sources are Ananjeva et al. (1990), Baig (1992), Khan (2002) and Baig et al. (2012). Hoser (2015) even claims priority with respect to the data albeit that his taxonomic scheme and all his characters have been copied from Baig (1992) and subsequent publications.

D) Hoser (2014c) on Uromastycinae

The manuscript of this paper was received by the journal on 2 November 2013, accepted on 15 May 2014, and finally published on 30 August 2014. It is presented in the following way: *Abstract* (including Keywords), *Introduction*, *Notes on the taxa named herein* followed by the description of taxa, *Conflict of Interest*, and *References Cited*. In total Hoser newly describes or resurrects within this publication two tribes, five genera, and four subgenera. Five of these taxa are monotypic.

The *Introduction* is relatively short and summarizes the taxonomic history of *Uromastyx* and gives Hoser's view on taxonomy, without any identified copied parts. However, two extraordinary statements should be discussed here. In terms of material used for his study, Hoser refers to the "inspection of live specimens at various facilities since 1993." Many *Saara* or *Uromastyx* species inhabit political unstable areas and it is very unlikely that there are live specimens of many important species, such as *S. asmussi* (Strauch, 1863), available at any facility Hoser might have visited since 1993. Therefore it is very probable that most of the data he presents are not from ex-

amined material, but from published sources. These sources are cited in the *Introduction* as "Significant studies relevant to the taxonomy of the Uromastycinae …" and include for example Hall (1999) and Swofford (2002), two general publications about statistical phylogenetic methods without any significance to the taxonomy of the group at all.

In his *Abstract* and *Introduction*, Hoser gives the impression that he is the first to use the approach by Pyron et al. (2013) to distinguish between Uromastycinae Theobald, 1868 and Leiolepidinae Fitzinger, 1843 on the subfamily level, but mentioning in passing that "some authors have already taken this step." This concept was used more than a decade ago by Macey et al. (2000a), in a paper not cited by Hoser. Instead, Hoser cites Macey et al. (2000b) on the trans-Tethys migration, which has hardly any relevance to uromasticine / leiolepidine taxonomy (only one species of *Uromastyx* and two species of *Leiolepis* were included in the study). We also note that the terms Uromastycinae and Leiolepidinae were used synonymously by different authors (e.g., Wilms & Böhme 2007: 436).

The entire first definition of Uromastycinae used by Hoser is identically phrased to Wilms et al. (2009:67; four lines), followed by the definitions of his two new tribes copied from the same source. The further detailed definition for this subfamily is not fully copied, but obviously taken from Boulenger's synopsis (Boulenger 1885: 405; 14 lines). All diagnosing parts of the subsequent definition of *Uromastyx* are entirely taken from various parts (text and key) of Wilms et al. (2009).

The first taxon Hoser describes is the subgenus *Uromastyx* (within *Uromastyx*) and the given diagnosis is taken from Wilms et al. (2009: 67 & 82; 35 lines copied for the genus *Uromastyx*, seven for the subgenus *Uromastyx*, of which 3.5 lines are within quotation marks). For his second, monotypic subgenus diagnosis, erected to accommodate *U. occidentalis* Mateo, Geniez, Lopez-Jurado & Bons, 1999, he uses eight lines directly copied from Wilms et al. (l.c.).

Even though Hoser quotes Wilms et al. (l.c., 3.5 lines) in the following diagnosis of *Aporoscelis*, the parts not directly quoted are also copied from that reference (two lines).

For his first new genus description Hoser is using a differential diagnosis separating his new taxon by the diagnosis of other taxa. Here, Hoser is summarizing the information given in the diagnostic key by Wilms et al. (2009: 82), followed by a description taken from Boulenger (1885: 405) with 26 lines copied. Also the diagnosis of the same taxon at a different rank (subgenus) is taken from Wilms et al. (2009, 11 lines copied). Within his new genus, Hoser describes two additional new subgenera. Even here all mentioned characters diagnosing these taxa are identical to Wilms et al. (2009: 82; 22 lines copied).

Diagnosing his second new genus, Hoser is following the same scheme of presenting a differential diagnosis. And again, all given characters, especially meristic characters (e.g., scale or whorl counts) are exactly the same as given in Wilms et al. (l.c.) and no other additional characters are provided. This description is followed by the subgenera to be included in the previously described genus. Again, all mentioned characters are exclusively taken from Wilms et al. (l.c.). The new genus is described by copying 14 lines from Wilms et al. (2009: 82–83), and subsequently three new subgenera are proposed using 44 lines from the same source.

While redescribing the genus *Saara* according to his new taxonomy, Hoser provides several characters to distinguish his new tribe, including *Saara*, from the tribe that includes *Uromastyx*. Here he is exclusively using the characters provided by Wilms et al. (2009: 81–82; 15 lines) for the three species forming the genus *Saara*. However, Hoser is splitting this genus into three distinct monotypic genera, including in addition to *Saara* the genus *Centrotrachelus* Strauch, 1863, which he resurrects to accommodate *S. asmussi*, and a new genus that only contains *S. loricatus* Blanford, 1874. In order to describe these two genera Hoser again uses Wilms et al. (2009: 81–82; 32 lines copied).

Finally, Hoser erects two new tribes to accommodate his proposed genera. The first tribe is described using three lines from Wilms et al. (2009:67) and 13 lines from Boulenger (1885:405). The second tribe is solely defined by characters given by Wilms et al. (2009: 67, 82 & 83; 15 lines).

In the *References Cited* section Hoser lists 154 references (three-and-a-half pages), giving the impression of a well-conducted, literature-based study. However, none of the references is cited in the running text (other than a lengthy list of general references as part of the *Introduction*), 78 of the references do not refer to *Uromastyx* taxonomy or distribution (several are concerned with *Leiolepis*, others with maintenance of *Uromastyx*), and 48 references do not refer to *Uromastyx* at all (including description of statistical methods, herpetofaunal lists outside the distribution of *Uromastyx*). The only references Hoser appears to actually use are those by Boulenger (1885) and Wilms et al. (2009), from which many lines are copied verbatim without appropriate attribution.

Summary Section D

The taxonomic basis for Hoser's proposals on Uromastycinae is a representation of nodes taken fron the phylogeny published by Pyron et al. (2013).

In total, Hoser's paper on *Uromastyx* contains an estimated 1490 lines, of which 490 lines are referenced publications and 1000 lines are text (inclusive of title and abstract). His diagnoses contribute 556 lines, of which 326

lines are diagnostic characters. With respect to the latter, of all diagnostic characters mentioned, 255 lines (78%) were identically phrased or copied from previously published research papers or reviews, with Wilms et al. (2009) and Boulenger (1885) being the main sources.

SUMMARY & CONCLUSIONS

We analyzed four of Hoser's publications on agamid lizards and found in all cases significant amounts of copied or plagiarized text to present the diagnostic characters (83% for Draconinae, 82% for Amphibolurinae, 77% for *Laudakia*, 78% for Uromastycinae). There is no harm per se in repeating diagnostic characters from the older literature and using them in order to define a genus. A species of *Draco* has a certain number of elongated ribs in the patagium and the nostrils are directed sidewards or upwards. Similarly, species of *Gonocephalus* have a gular fold and *Chlamydosaurus kingi* possess a frill. There exist only a limited number of different expressions to present certain character sets. However, we think that Hoser's approach is on a different level that most scientists and editors would consider a sort of plagiarism. We found paragraphs that clearly show that Hoser's presentation of the diagnosis is a result of a copy-and-paste procedure with typographical errors in exactly the same place in his text where they occurred in the original publication. Furthermore, the direct uses of statements from the older literature lack attribution; merely including titles in a bibliography is not attribution. Meristic characters or statistical values tend to be given with the identical numbers of a source paper (for examples, see the sections on *Draco* or *Uromastyx*) although it is clear that Hoser neither took any measurements nor conducted a statistical analysis, as he would not have had access to the same specimens (or any specimens for that matter).

By pure repetition of character sets, which are often as old as 125 years, several of Hoser's diagnoses are rendered inaccurate, inconsistent, or even false. Often a diagnosis consists of more than one character set taken verbatim from two different publications; sometimes as much as half a page is copied in full, or long descriptions are taken directly from a previous publication. In at least three cases (*Laudakia*, *Paralaudakia lehmanni*, *Hypsilurus*), sets of characters that were copied by Hoser had been published in an identical or near-identical manner before, but the original sources are not cited at all!

We were able to identify the sources of most (~ 90%) of the diagnostic characters used by Hoser (2012a, 2013, 2014b, c). If the percentage of word-for-word copying of Hoser's diagnostic characters section is evaluated, this amounts to approximately 80% of his presentation. Even if the whole diagnoses are taken into account for which Hoser typically uses long sentences that have nothing to do with the actual definition of the taxon, the percentage still stands at over 60%. With respect to Hoser's full publications considered here, approximately 20% (*Laudakia* paper 11%) of the text constitutes a verbatim copy from other sources. In several cases copied sections exceed 100 lines of identical text, and often full descriptions of species or excerpts from publications concerned with the phylogeny or taxonomy of agamid lizards are repeated word-for-word.

Hoser's papers often contain an exhaustive bibliography which gives the impression of a properly performed literature search. However, we found that actually fewer than 50 publications (out of several hundred referenced) were used. Three publications used are not referenced at all, and none of the publications by his fellow Australian Jane Melville (authored or co-authored) was cited or used, although these contain phylogenies of *Laudakia* and *Diporiphora* as well as nomenclatural proposals preceding those of Hoser. The use of unreferenced material is a clear breach of commonly accepted editorial standards and should be avoided by all means. Hoser's papers should not have passed any peer review based on the amount of copied text and in our opinion his work constitutes in several cases a form of plagiarism.

Analysing Hoser's proposed nomenclature we can identify cases where a name is preoccupied and unavailable, where a name is being resurrected that was resurrected before, where names are used that had been very recently synonymized with other genera but for which the literature was overlooked or disregarded. In one case Hoser assigns a name to a genus that does not include the type species which he places into another genus. In other cases, he produces *nomina nuda* or resurrects a *nomen oblitum* incorrectly. He further restricts a type locality without identifying a type specimen from that area and selects a holotype for a newly described species that has a bifurcated tail without any mentioning of this particular feature.

With respect to taxonomy, in each of the four papers we find examples of wrong diagnoses, falsely attributed species, and misinterpretation of previously published taxonomic studies. Furthermore, Hoser omitted several genera in his classification schemes (e.g. *Harpesaurus*, *Thaumatorhynchus*, *Psammophilus* and *Tympanocryptis*) as well as many species (e.g. species of *Phrynocephalus* and *Lophognathus*). Presented as they are, Hoser's taxonomic schemes for the subfamilies Amphibolurinae and Draconinae, as well as his division of the genera *Laudakia* and *Uromastyx*, just constitute a grouping and naming exercise within the confines of a particular published phylogeny he chooses to follow. The slightest changes in these phylogenies will render them false, in particular as molecular data have not been used to study all genera and species under consideration. Hence, Hoser's taxonomies and nomenclature acts are highly unstable and little help-

ful for species assigment. A herpetologist trying to assign a newly collected specimen or an existing museum voucher to a specific taxon will still have to look for the original or subsequent publications where keys are available, and would have to revert to Hoser's paper(s) only to determine his proposed nomenclature – if those names were available. Kaiser et al. (2013) and Kaiser (2013) suggested a suppression of all Hoser names to prevent such case and produced a list with recommended appropriate names. With respect to the taxa dealt with in the present paper we propose to suppress Hoser's names completely and recommend the usage of generally accepted names which can be found in the Reptile Database (Uetz & Hošek 2015).

While available names have to be used according to the *Code*, a taxonomy does not necessarily have to be accepted. If we were to work in the same way as Hoser does we could claim here that *Gonocephalus mjobergi* and *Ptyctolaemus* share a common character, namely longitudinal gular folds. We could further claim to consider this a synapomorphy not shared by the *Japalura variegata* / *Oriotiaris* group, propose a new tribe excluding *Japalura* / *Oriotiaris* with *Ptyctolaemus gularis* (Peters, 1864) as the type species and name it accordingly. While our tribe would have a common character to define it, two of Hoser's tribe diagnoses, which are defined by their content rather than common characters, would become invalid. Equally we could claim that *Hypsicalotes kinabaluensis* (de Grijs, 1937) has a unique set of characters (which it has) that distinguishes the genus from all other Draconinae and remove it from Hoser's tribe, only to name a new tribe.

Although this paper is mainly meant to analyze Hoser's taxonomy and nomenclature we have to address some issues with regard to the *Code*. There is no requirement for a publication to be peer-reviewed or to comply with any other commonly accepted editorial standards. The ethics recommended by the *Code* do not have to be adhered to. Even a photograph and short description of the colouration followed by a new name published in a daily newspaper would qualify as valid and therefore the name would be considered available. Zoobank is the official registry of the ICZN. Everyone can register with Zoobank (a viable approach and we hope it will stay like this) and subsequently register nomenclatural acts. However, Zoobank is not curated and there is no review process in place to check the correctness of submitted data. This literally invites pure naming exercises by "harvesting" nodes (nomenclatural vandalism) from a previously published phylogenetic tree. At the end of November 2015, Hoser had 873 nomenclatural acts registered with Zoobank, which on the face of it leads to two different nomenclatures for many reptilian taxa as his names are not accepted by the overwhelming majority of the herpetological community.

The ICZN needs to implement provisions to prevent unscientific and unethical publication of nomenclatural proposals to become available. We are convinced that Hoser is abusing the system. The preceding examples provide sufficient evidence to demonstrate his abuses. We strongly recommend that the ICZN uses their plenary power to suppress all of Hoser's nomenclatural acts published in the *Australasian Journal of Herpetology*. We feel that, if this step is not taken, a large part of the herpetological community will – with great respect for the ICZN and with great regret – continue to use the alternative nomenclatural system of the Reptile Database as a reference for available names.

CONFLICT OF INTEREST

All four authors have submitted taxonomic papers on agamid lizards including nomenclatural changes without acknowledging Hoser's nomenclature or referencing his publications. Our own publications have been extensively used verbatim by Hoser without asking for permission to do so. The authors therefore have a personal interest to put this on public record.

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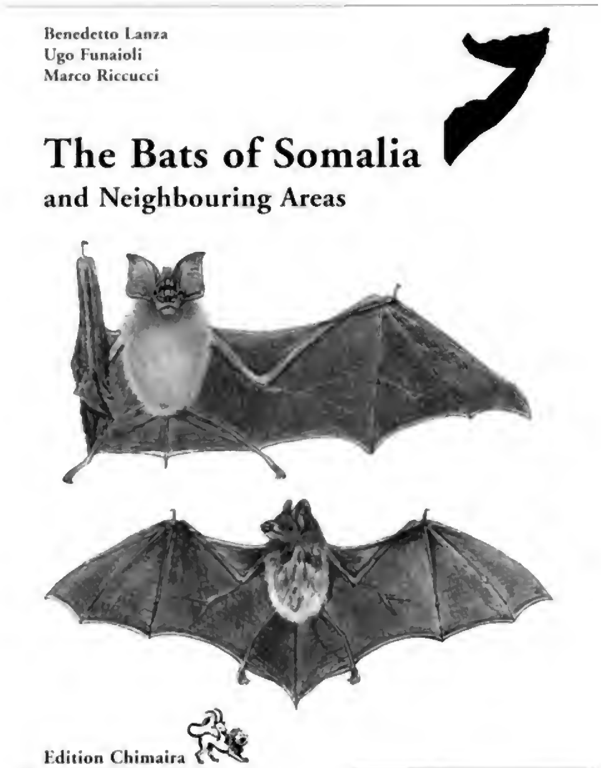

In this voluminous book the authors cover every aspect of the 79 bat species they found associated with Somalia and adjacent areas. There are introductory chapters to the order Chiroptera (with key to the two suborders), suborder Megachiroptera, followed by suborder Microchiroptera with a key to the families, then family with key to the genera, and genus with keys to the species, before each species is discussed individually. Each of these chapters follows a similar structure with "derivatio nominis" (name derivations and etymology), "composition and distribution", and "distinctive characters". Family and genus chapters add paragraphs on "type genus [species]", "iconography" (= a listing of the figures associated with that chapter), "synonymy" and "common names", "taxonomy", "echolocation calls," where available, "biology", "Somali records" and "Personal observations." Within this pattern the authors provide a great amount of detail on the species, all illustrated with a color drawing of the bat with one wing outstretched (sometimes replaced by color photographs of mounted specimens), up to three (!) sets of pen-and-ink skull drawings per species, nicely showing individual variation, and variously photographs or drawings of penis, bacula, palatal ridges, or details of dentition, skull, tragi or noseleaves depending on the family's special characteristics. Quite a bit of information is contained in the name derivations, from the Greek and Latin roots to interesting details on naturalists or hunter-collectors the bat may be named after, and - where available - the bat's biology. Common names listed include English and Italian names but no local Somali names. Well-organized tables identify many of the individual measurements of the 3650 museum specimens examined, all given with museum acronyms and numbers, and summary statistics.

At the end of the book, under "Addenda," two species, *Kerivoula smithii* and *Laephotis wintoni* are added as "occurring in areas nearby Somalia", followed by 32 detailed distribution maps, some of which covering more than one species, with numbered point localities, all of which identified by name (!) in separate legends. This is then followed by the Acknowledgements, a detailed six-page Gazetteer with many useful spelling variants and 16 pages of References including literature as recent as some of the species entries from Happold and Happold's 2013 bat volume in the new *Mammals of Africa* series, which is greatly complemented by this new book.

As if this wasn't enough, the book concludes with a separate section by Funaioli and Lanza entitled "An outline of the geography of Somalia" that provides the smaller distribution maps in the main section with much more detail regarding political subdivisions, average yearly rains, and a "Sketch map of the vegetation [zones] of the Somali Democratic Republic," the latter nicely illustrated with one black & white and 17 color photographs and some more general information on flora and fauna of Somalia. A separate reference section concludes this chapter, which is especially valuable, as it is next to impossible to travel safely in Somalia at this time.

If there was ever a modern "Rolls Royce"- equivalent of a "Bats of ..."-book, with all the possible bells and whistles, this must be it. Yet, the publisher, Edition Chimaira, somehow managed to accommodate every lavish aspect of this book and seemingly all special wishes of the authors in a still portable size, printed on durable glossy paper, which does justice to all the different types of illustrations, but keeps the price for this rather specialized books within reasonable limits. May this volume find its way to all those interested in Somalia or the fauna of the Horn of Africa in general and bats in particular, and may it serve as an exemplarily illustrated and detailed account for this part of Africa, both areas where the bat-volume of Kingdon's *Mammals of Africa* falls short.

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